THE TAXONOMY OF THE FAMILY PARAMPHISTOMIDAE FISCHOEDER, 1901 WITH SPECIAL REFERENCE TO THE MORPHOLOGY OF SPECIES OCCURRING IN RUMINANTS

by

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ABSTRACT

The thesis consists of two main sections and deals with taxonomic studies of the family Paramphistomidae Fischoeder, 1901.

The first section reviews the various schemes of classification published for the group. The various characters both morphological and histological, employed in the classification of members of the family are discussed and assessed. The value of tegumental papillae as specific characters is recognised and scanning electron micrographs of the different types observed on the anterior end of some species are provided.

The second section is the systematic part and deals with discussion of ten genera occurring mainly in ruminants. The history of each genus is given and the species are described, illustrated and their synonymies discussed. The genus Paramphitomum Fischoeder, 1901 is redefined and only nine species, including one as new are considered valid. The genera Liorchis Velichko, 1966 and Srivastavaia Singh, 1970 are synonymized with Paramphistomum Fischoeder, 1901. The genus Calicophoron Näsmark, 1937 is redefined and revised to contain only 12 species some of which in new combinations. The genus Bothriophoron (Stiles and Goldberger, 1910) Grétillat, 1958 is considered a synonym of Calicophoron Näsmark, 1937. The genus Gigantocotyle Näsmark, 1937 is redefined and contains only four valid species. The subgenus Explanatum Fukui, 1929 is raised to full generic rank, redefined to contain only three valid species. The genus Cotylophoron Stiles and Goldberger, 1910 is revised to contain only seven valid species. The genus Orthocoelium (Stiles and Goldberger,

1910) Price and McIntosh, 1953 is revised, only nine species are considered valid and two new species are added, one of the latter is appended as a publication. The genera Ceylonocotyle Näsmark, 1937 and Cochinocotyle Gupta and Guta, 1970 are considered synonyms of Orthocoelium (Stiles and Goldberger, 1910) Price and McIntosh, 1953. Two new genera are erected and appended as publications. These are Bilatorchis which contains a single species described as new and Leiperocotyle which contains three species, two in new combinations and one as a nomen novum. Of the three species assigned to the genus Stephanopharynx Fischoeder, 1901 only one, S. compactus Fischoeder, 1901 is considered valid. The one and only species of the genus Balanorchis, B. anastrophus Fischoeder, 1901 is redescribed, illustrated and for the first time, its histological features are elucidated. Keys to the species of the above genera are provided and scanning electron micrographs of the tegumental surfaces of some species are shown. The zoogeographical affinities of the paramphistomids of ruminants are discussed and a list of the hosts and localities of the species is given.

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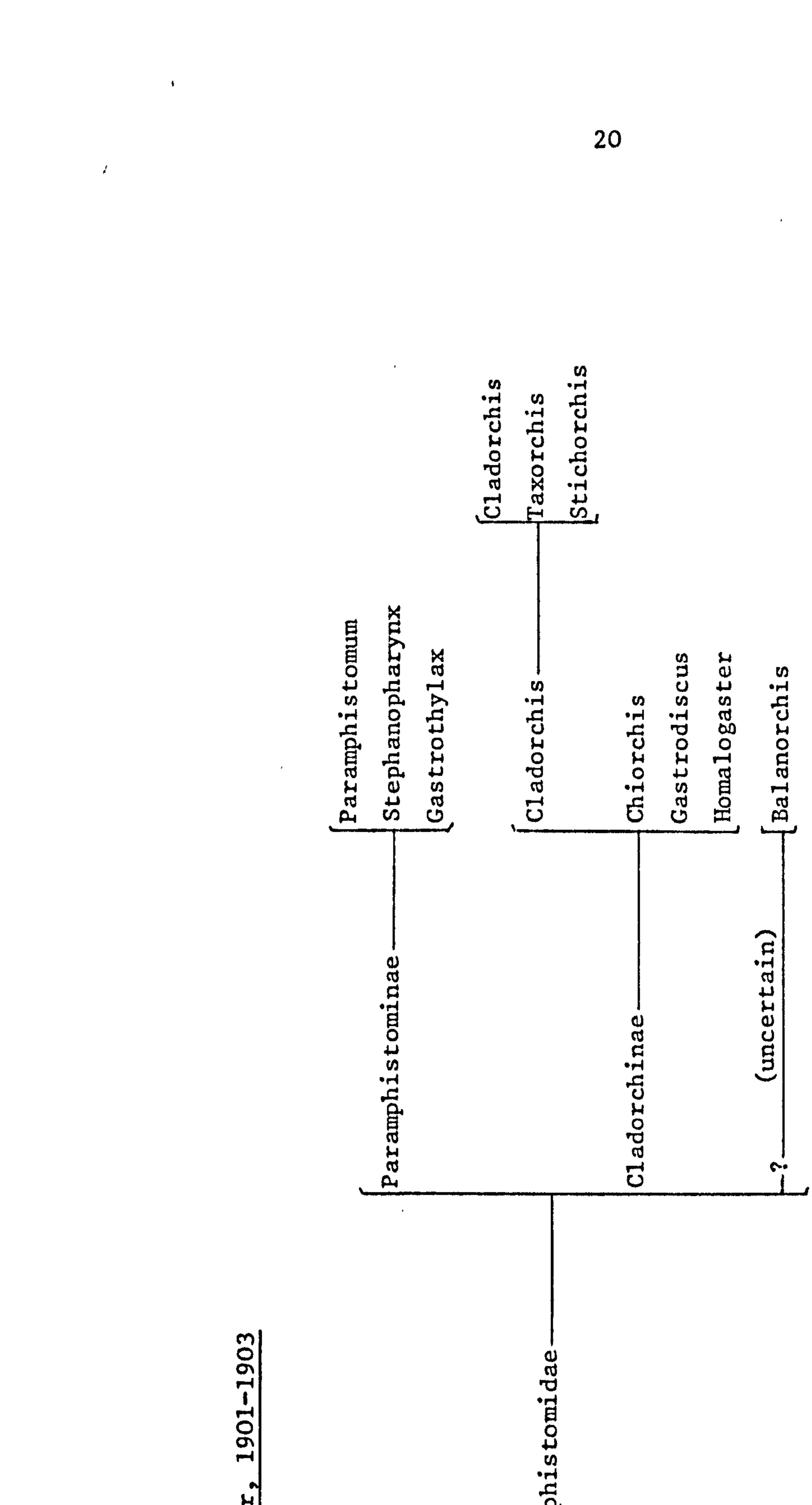
1. INTRODUCTION

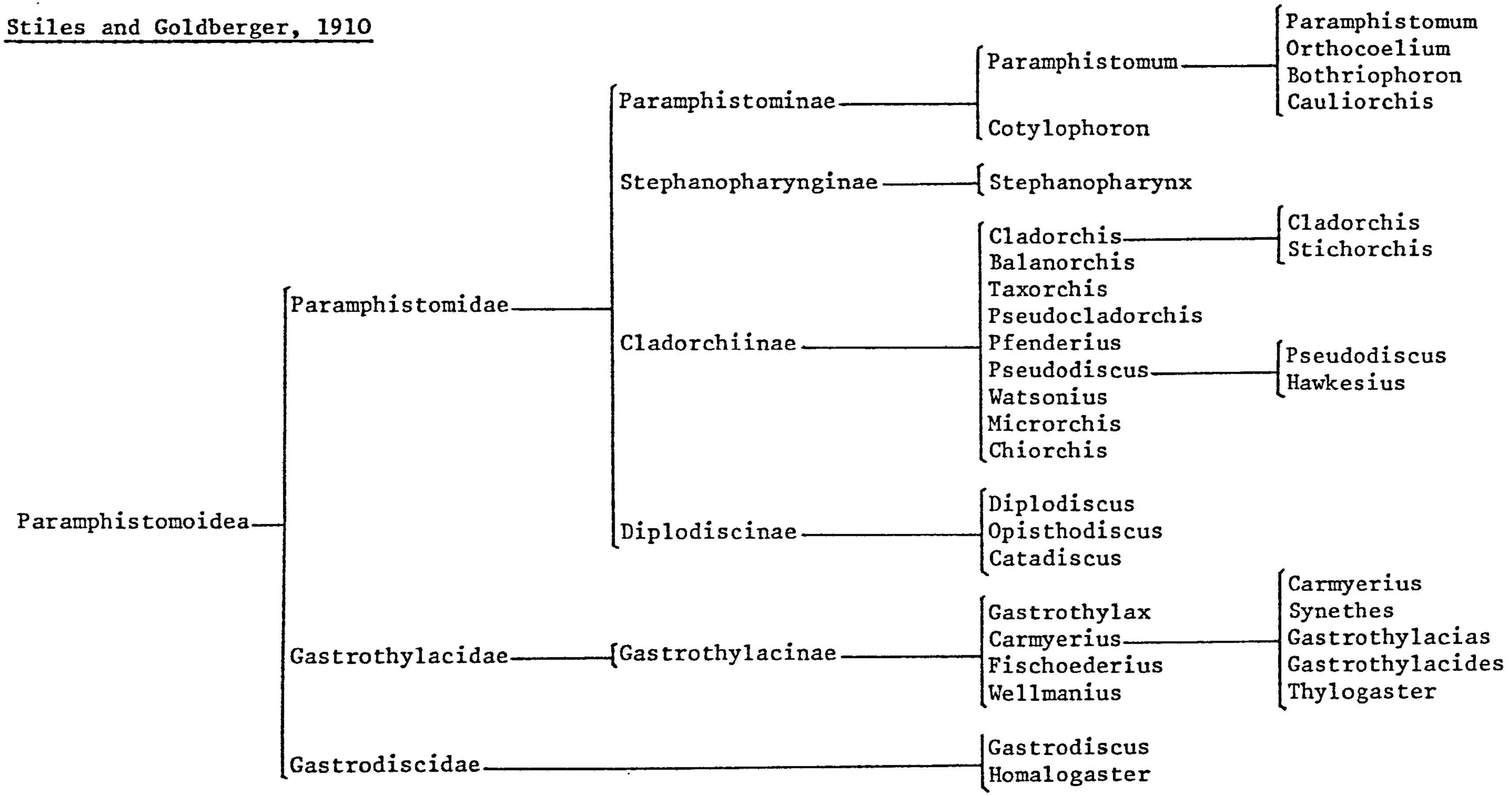
The family Paramphistomidae

The family Paramphistomidae was established by Fischoeder (1901, 1902, 1903) for two new subfamilies, Paramphistominae and Cladorchiinae. Stiles and Goldberger (1910) erected the superfamily Paramphistomoidea and assigned to it three families, Paramphistomidae Fischoeder, 1901; Gastrodiscidae and Gastrothylacidae, the latter two were established as new families. They restricted the family Paramphistomidae Fischoeder, 1901 to contain the subfamilies Paramphistominae Fischoeder, 1901; Cladorchiinae Fischoeder, 1901 and Diplodiscinae Cohn, 1904. Since then several additions and changes to the structure of the family have taken place. The major systems of classification proposed by various authors for the group apart from those of Fischoeder (1901-1903) and Stiles and Goldberger (1910) are those of Stunkard (1917, 1929), Maplestone (1923), Fuhrmann (1928), Fukui (1929), Travassos (1934), Näsmark (1937), Southwell and Kirshner (1937), Szidat (1939), Skrjabin (1949), Yamaguti (1958, 1971) and Baer and Joyeux (1961). These are summarized in the following charts.

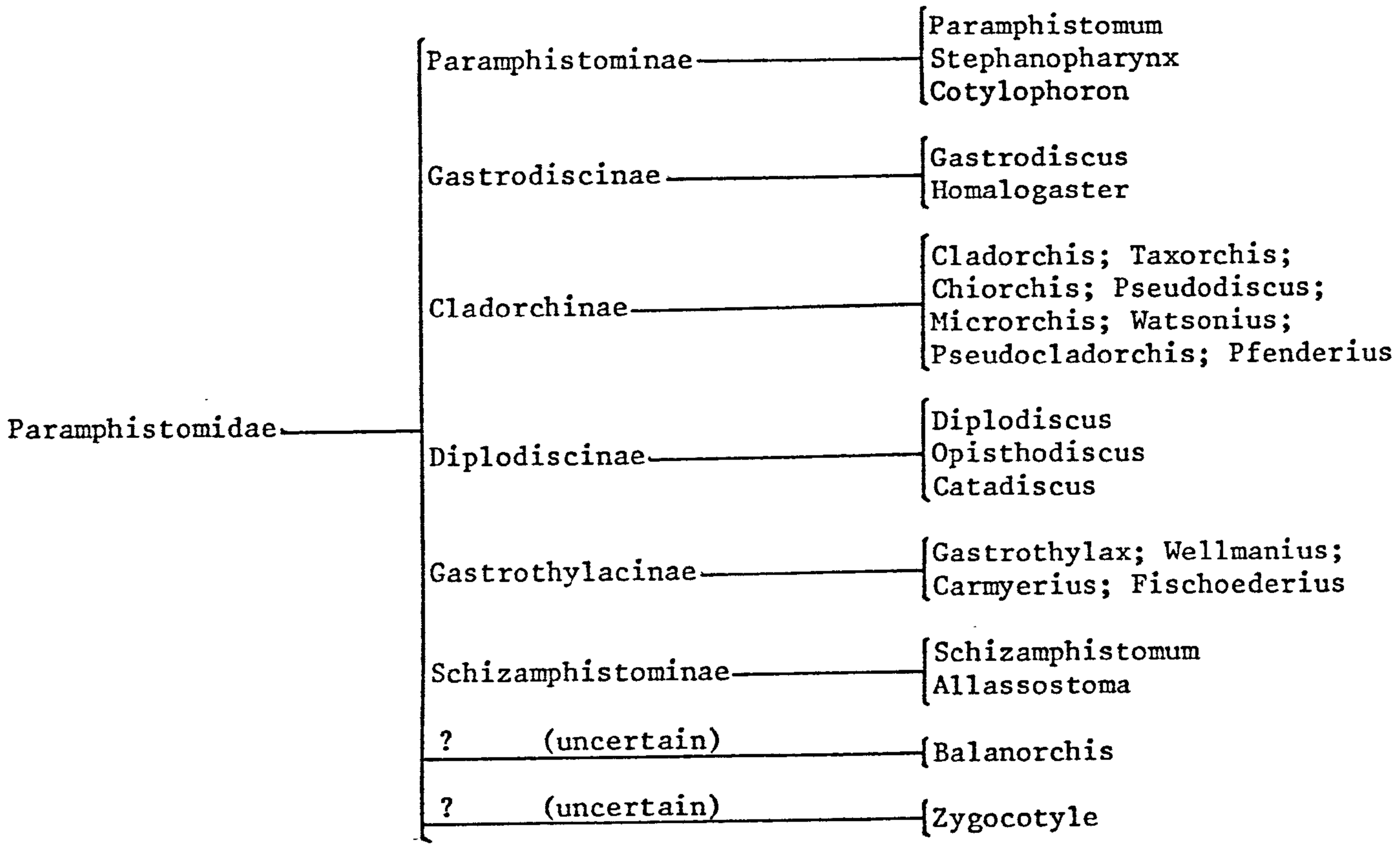
Fischoeder, 1901-1903



Stiles and Goldberger, 1910



Stunkard, 1917



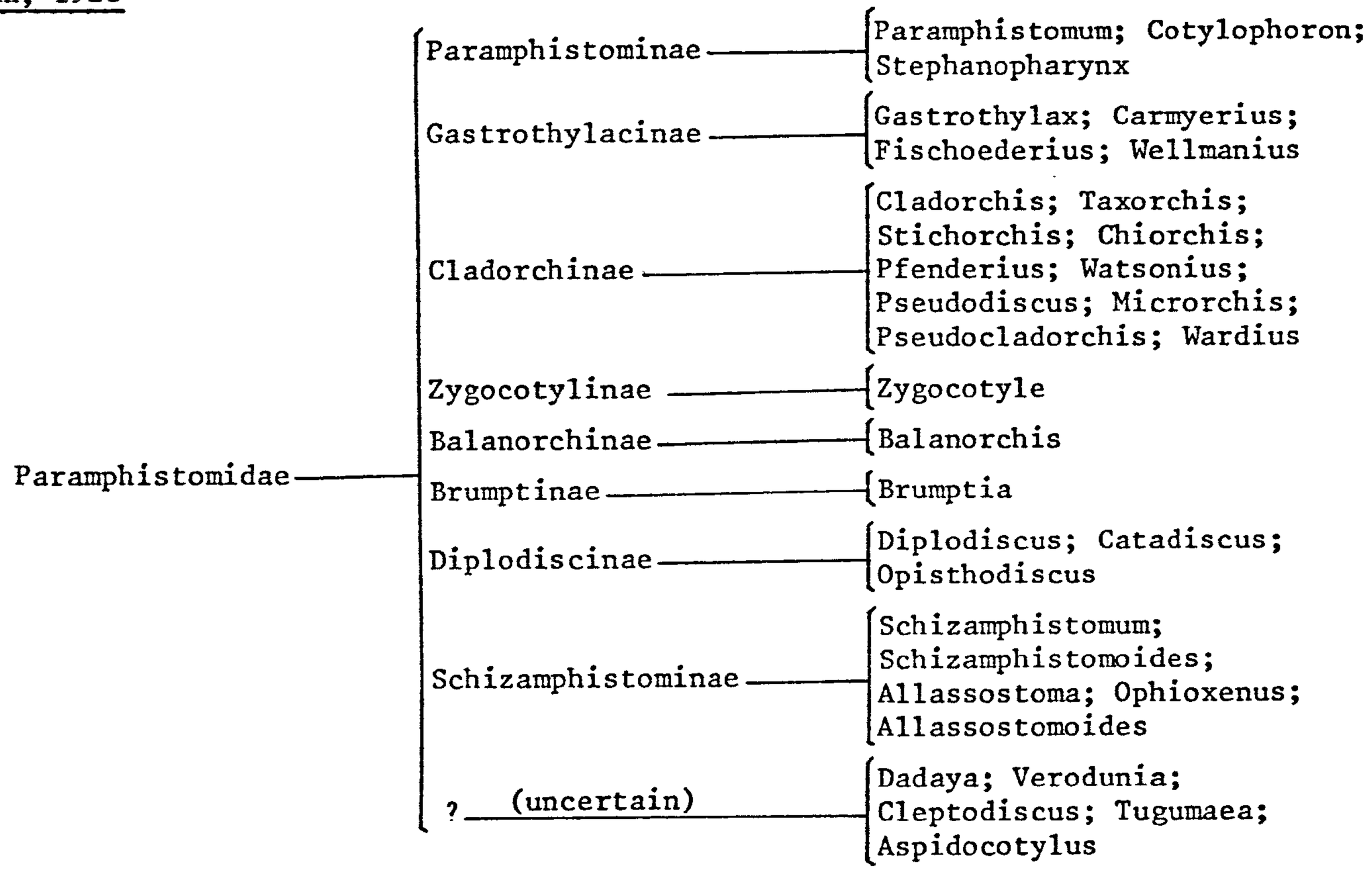
Maplestone, 1923

Amphistoma
- Gastrothylacidae
  - Paramphistomidae
    - Paramphistominae
      - Paramphistomum
      - Cotylophoron
    - Cladorchinae
      - Cladorchis
      - Pseudodiscus
      - Balanorchis
      - Pfenderius
      - Chiorchis
      - Taxorchis
  - Stephanopharyngidae
    - Stephanopharyngeae
      - Stephanopharynx
  - Gastrothylacinae
    - Gastrothylax
    - Carmyerius
    - Fischoederius
  - Gastrodiscidae
    - Gastrodiscus
    - Gastrodiscoides
    - Homalogaster
  - ? (uncertain)
    - Brumptia

Stunkard, 1925

- Paramphistomidae
  - Paramphistominae — Paramphistomum; Cotylophoron; Stephanopharynx
  - Cladorchinae — Cladorchis; Taxorchis; Stichorchis; Chiorchis; Pfenderius; Watsonius; Wardius; Pseudocladorchis; Microrchis; Pseudodiscus
  - Schizamphistominae — Schizamphistomum; Allassostomoides; Schizamphistomoides; Allassostoma
  - Gastrothylacinae — Gastrothylax; Carmyerius; Fischoederius
  - Zygocotylinae — Zygocotyle
  - Balanorchinae — Balanorchis
  - Brumptinae — Brumptia
  - Diplodiscinae — Diplodiscus; Catadiscus; Opisthodiscus
  - Gastrodiscinae — Gastrodiscus; Homalogaster; Gastrodiscoides

Fuhrmann, 1928



Fukui, 1929

- Amphistomata
  - Paramphistomatidae
    - Paramphistomatinae
      - Paramphistomatinea
        - Paramphistoma
          - Paramphistoma
          - Cotylophoron
          - Buxifrons
          - Explanatum
        - Gastrothylax
          - Gastrothylax
          - Fischoederius
          - Carmyerius
      - Stephanopharynginea
        - Stephanopharynx
      - Pseudodiscinea
        - Pseudodiscus
          - Pseudodiscus
          - Watsonius
    - Cladorchinae
      - Cladorchis
        - Cladorchis
        - Stichorchis
      - Taxorchis
      - Chiorchis
        - Chiorchis
        - Helostomatis
        - Microrchis
    - Zygocotylinae
      - Zygocotyle
    - Brumptinae
      - Brumptia
    - Balanorchinae
      - Balanorchis
    - Pfenderinae
      - Pfenderius; Tugumaea
    - Schizamphistomatinae
      - Schizamphistoma; Allassostoma; Schizamphistomoides
    - Diplodiscinae
      - Diplodiscus; Catadiscus; Opisthodiscus
    - Gastrodiscinae
      - Gastrodiscus; Homalogaster; Gastrodiscoides
    - Dadayinae
      - Dadayius; Denticauda
  - Opistholebetidae
    - Opistholebetinae
      - Opistholebis
    - Gyliaucheninae
      - Gyliauchen
  - Angiodictyidae
    - Angiodyctium; Octangium; Microscaphidium; Deutobaris; Polyangium
  - Opisthoporidae
    - Opisthoporus

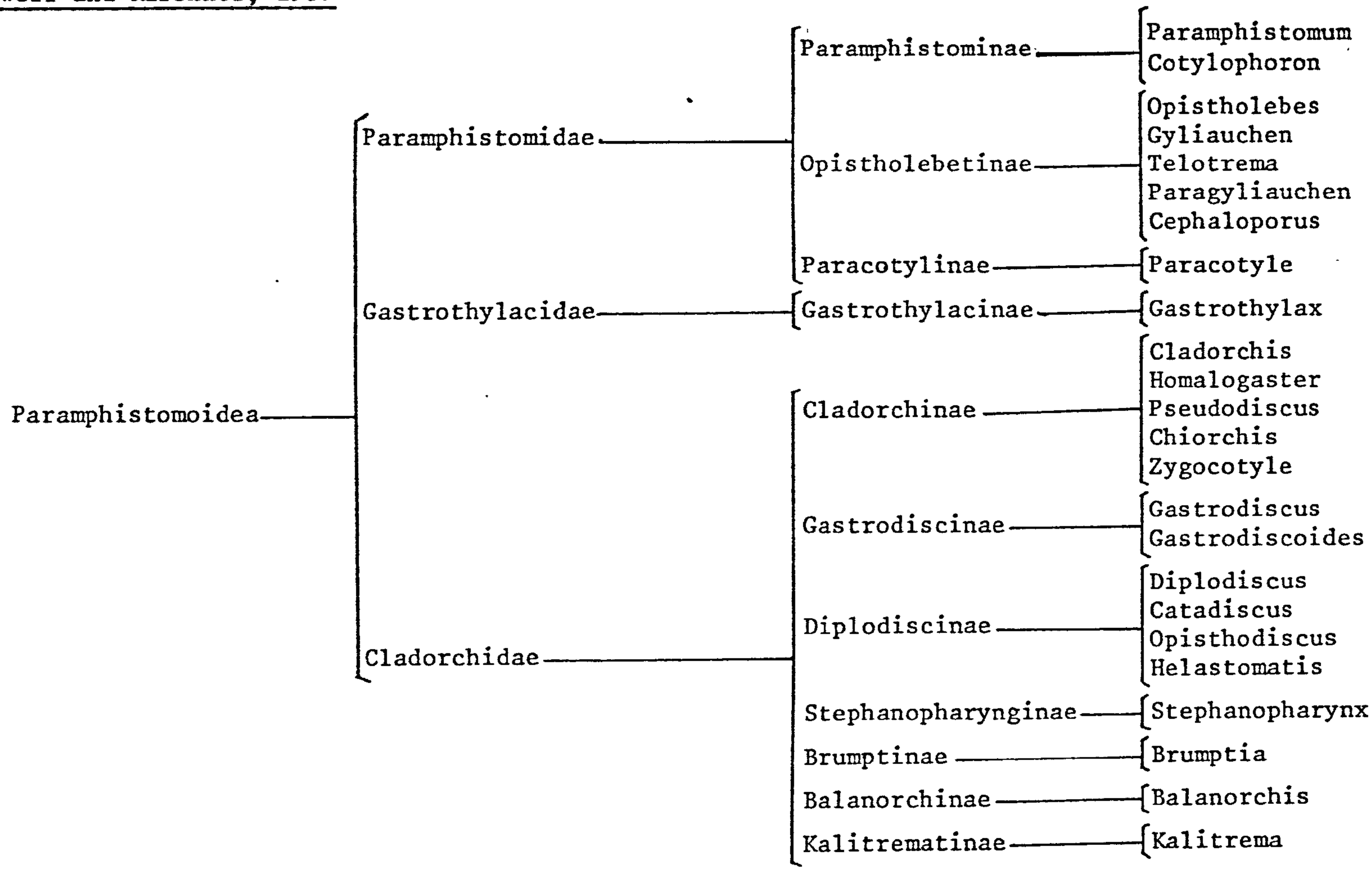
Travassos, 1934

- Paramphistomidae
  - Paramphistominae
    - Paramphistomum
      - Paramphistomum
      - Cauliorchis
    - Cotylophoron
  - Gastrothylacinae
    - Gastrothylax
    - Carmyerius
    - Fischoederius
  - Stephanopharynginae
    - Stephanopharynx
  - Zygocotylinae
    - Zygocotyle
    - Stunkardia
  - Balanorchinae
    - Balanorchis
  - Kalitrematinae
    - Kalitrema
  - Cladorchinae
    - Cladorchis
    - Stichorchis
    - Taxorchis
    - Pseudodiscus
    - Hawkesius
    - Wardius
    - Chiostichorchis
    - Pfenderius
    - Tugumaea
    - Chiorchis
    - Schizamphistomum
    - Allassostoma
    - Allassostomoides
    - Cleptodiscus
    - Schizamphistomoides
    - Ophioxenus
    - Microrchis
    - Pseudocladorchis
    - Dadaytrema
    - Travassosinia
    - Helostomatis
    - Dadayius
    - Nematophila
  - Diplodiscinae
    - Diplodiscus
    - Megalodiscus
    - Opisthodiscus
    - Catadiscus
  - Brumptinae
    - Brumptia
- Paramphistomoidea
  - Gastrodiscidae
    - Gastrodiscus
    - Gastrodiscoides
    - Homalogaster
  - Opistholebetidae
    - Opistholebis
  - Gyliauchenidae
    - Gyliauchen
    - Paragyliauchen
    - Telotrema
  - Microscaphidiidae
    - Microscaphidium
    - Polyangium
    - Angiodyctium
    - Octangium
    - Deutobaris
    - Parabaris
    - Hexangium
    - Nephrobius
  - Cephaloporidae
    - Cephaloporus
    - Plectognathotrema

Näsmark, 1937

- Paramphistomidae
  - Paramphistominae — Paramphistomum; Gigantocotyle; Calicophoron; Cotylophoron; Ugandocotyle; Ceylonocotyle; Nilocotyle; Buxifrons; Macropharynx
  - Gastrothylacinae — Gastrothylax
  - Brumptiinae — Brumptia
  - Watsoniinae — Watsonius
  - Gastrodiscinae — Gastrodiscus; Homalogaster; Gastrodiscoides
  - Pseudodiscinae — Pseudodiscus
  - Stephanopharynginae — Stephanopharynx
  - Pseudocladorchinae — Pseudocladorchis
  - Schizamphistominae — Schizamphistomum; Allassostomoides; Schizamphistomoides; Allassostoma; Ophioxenos; ?Cleptodiscus; ?Dadaytrema
  - Stichorchinae — Stichorchis
  - Cladorchinae — Cladorchis; Taxorchis; Chiorchis; Microrchis
  - Pfenderinae — Pfenderius; Tegumaea
  - Diplodiscinae — Diplodiscus; Opisthodiscus
  - Balanorchiinae — Balanorchis
  - Zygocotylinae — Zygocotyle

Southwell and Kirshner, 1937



Szidat, 1939

- Paramphistomata
  - Paramphistomidae
    - Paramphistominae
      - Paramphistomum; Cotylophoron; Stephanopharynx
    - Gastrothylacinae
      - Gastrothylax; Wellmanius; Fischoederius
    - Gastrodiscinae
      - Gastrodiscus; Homalogaster; Gastrodiscoides
    - Balanorchinae
      - Balanorchis
    - Chiorchinae
      - Chiorchis
    - Cladorchinae
      - Cladorchis; Taxorchis; Stichorchis; Watsonius; Wardius; Hawkesius; Brumptia; Pfenderius; Pseudodiscus
    - Zygocotylinae
      - Zygocotyle
    - Diplodiscinae
      - Diplodiscus; Catadiscus; Opisthodiscus
    - Schizamphistominae
      - Schizamphistomum; Ophioxenus; Schizamphistomoides; Stunkardia; Allassostoma; Allassostomoides
    - Dadaytreminae
      - Dadaytrema; Dadayius; Microrchis; Pseudodiplodiscus; Travassosinia; Pseudocladorchis; Parabaris
    - Opistholebetinae
      - Opistholebis; Paracotyle; Gyliauchen; Paragyliauchen
  - Mesotremidae
    - ?Kalitrema; Flagellotrema; Helostomatis; Neocladorchis; Heterolebis; Petalocotyle; Nicollodiscus; Orientodiscus
  - Angiodictyidae
  - Notocotylidae

Skrjabin, 1949

- Paramphistomatata
  - Cladorchoidea
    - Paramphistomatoidea
      - Paramphistomatidae: Paramphistomum; Cotylophoron; Gigantocotyle; Calicophoron; Ugandocotyle; Ceylonocotyle; Nilocotyle; Buxifrons; Macropharynx
      - *Gastrothylacidae*: Gastrothylax; Carmyerius; Fischoederius
    - Cladorchidae
      - Cladorchinae: Cladorchis; Taxorchis; Stichorchis; Chiostichorchis
      - Pfenderiinae: Pfenderius; Tugumaea
      - Balanorchinae: Balanorchis
      - Pseudodiscinae: Pseudodiscus
      - Kalitrematinae: Kalitrema
      - Cleptodiscinae: Cleptodiscus
      - Stichorchinae: Stichorchis
    - Diplodiscinae
      - Diplodiscinae: Diplodiscus; Catadiscus; Megalodiscus; Dermatemytrema
      - *Opisthodiscinae*: Opisthodiscus
      - Schizamphistomatinae: Schizamphistomum; Chorchis; Schizamphistomoides; *Ophioxenus*; Allassostomoides; Microrchis; Travassosinia; Dadaytrema; Allassostoma; Neocladorchis
      - Helostomatinae: Helostomatis; Protocladorchis
      - Nematophilinae: Nematophila; Orientodiscus
      - Watsoniinae: Watsonius; *Hawkesius*
      - Dadayinae: Dadayius
      - Zygocotylinae: Zygocotyle; Stunkardia
      - Nicollodiscinae: Nicollodiscus
    - Gastrodiscidae
      - Gastrodiscinae: Gastrodiscus; Homalogaster; Gastrodiscoides
    - Stephanopharyngidae
      - Stephanopharynginae: Stephanopharynx
    - Brumptidae
      - Brumptinae: Brumptia
  - Microscaphidioidea
    - Microscaphidiidae: Microscaphidium; Polyangium; *Angiodictyum*; *Octangioides*; Octangium; Deuterobaris; Hexangitrema; Hexangium; Parabaris
  - Gyliauchenoidea
    - Gyliauchenidae: Gyliauchen; Paragyliauchen; Telotrema
    - Metacetabulidae: Metacetabulum

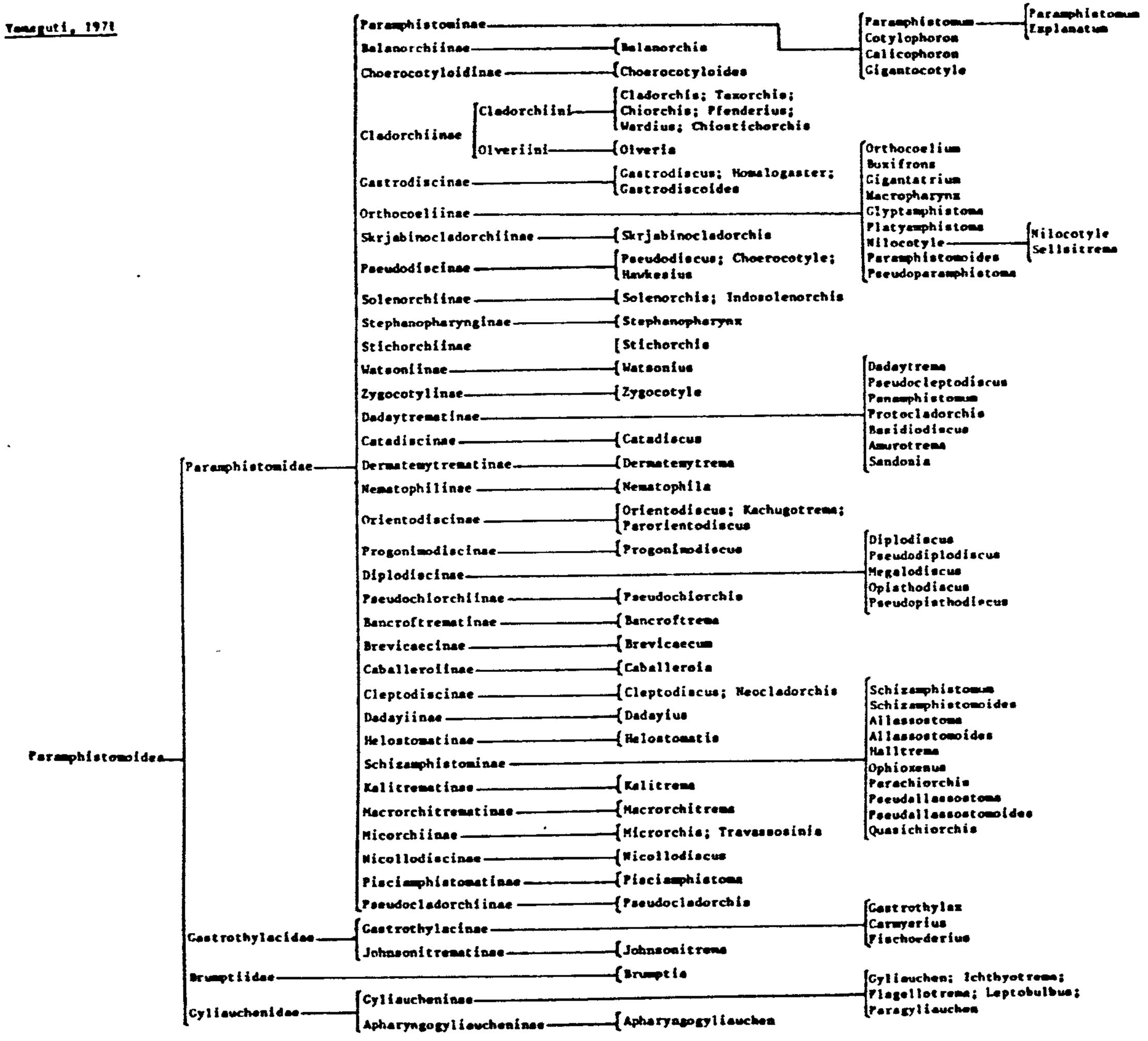
Yamaguti, 1958

- Paramphistomidae
  - Paramphistominae
    - Paramphistomini
      - Paramphistomum
        - Paramphistomum
        - Explanatum
      - Cotylophoron; Calicophoron;
      - Ugandocotyle
    - Ceylonocotylini
      - Ceylonocotyle; Macropharynx;
      - Buxifrons; Pseudoparamphistoma;
      - Glyptamphistoma; Platyamphistoma;
      - Paramphistomoides; Gigantatrium;
      - Nilocotyle
        - Nilocotyle
        - Sellsitrema
  - Diplodiscinae
    - Diplodiscus
    - Catadiscus
    - Megalodiscus
    - Opisthodiscus
    - Pseudopisthodiscus
  - Balanorchiinae
    - Balanorchis
  - Brumptiinae
    - Brumptia
  - Cladorchiinae
    - Cladorchiini
      - Cladorchis; Chiorchis; Taxorchis;
      - Chiostichorchis; Wardius;
      - Pfenderius; Stichorchis
    - Olveriini
      - Olveria
  - Schizamphistominae
    - Schizamphistomum
    - Schizamphistomoides
    - Allassostoma
    - Allassostomoides
    - Halltrema
    - Nematophila
    - Ophioxenus
    - Parachiorchis
    - Pseudallassostoma
    - Quasichiorchis
  - Gastrodiscinae
    - Gastrodiscus; Homalogaster; Gastrodiscoides
  - Gastrothylacidae
    - Gastrothylax; Carmyerius; Fischoederius
  - Johnsonitrematinae
    - Johnsonitrema
  - Pseudodiscinae
    - Pseudodiscus; Hawkesius; Watsonius
  - Solenorchiinae
    - Solenorchis; Indosolenorchis
  - Stephanopharynginae
    - Stephanopharynx
  - Zygocotylinae
    - Zygocotyle; Stunkardia
  - Dermatemytrematinae
    - Dermatemytrema
  - Pseudochiorchiinae
    - Pseudochiorchis
  - Dadayiinae
    - Dadayius
  - Dadaytrematinae
    - Dadaytrema; Orientodiscus; Protocladorchis
  - Helostomatinae
    - Helostomatis
  - Kalitrematinae
    - Kalitrema
  - Macrorchitrematinae
    - Macrorchitrema; Pisciamphistoma
  - Microrchiinae
    - Microrchis
  - Nicollodiscinae
    - Nicollodiscus
  - Pseudocladorchiinae
    - Pseudocladorchis
- Gyliauchenidae
  - Gyliaucheninae
    - Gyliauchen; Flagellotrema; Ichthyotrema; Paragyliauchen
  - Apharyngogyliaucheninae
    - Apharyngogyliauchen

Baer and Joyeux, 1961

- Paramphistomatoidea
  - Paramphistomatidae
    - Paramphistomatinae
      - Paramphistomum; Cotylophoron; Stephanopharynx
    - Diplodiscinae
      - Diplodiscus; Opisthodiscus; Dermatemytrema
    - Zygocotylinae
      - Zygocotyle; Stunkardia; Solenorchis
    - Cladorchiinae
      - Cladorchis; Balanorchis; Allassostoma; Halltrema Allassostomoides; Wardius; Amurotrema; Chiostichorchis; Cleptodiscus; Dadaytrema; Schizamphistoma; Nematophila; Schizamphistomoides; Olveria; Protocladorchis; Pfenderius; Orientodiscus; Stichorchis; Pseudoparamphistoma
    - Pseudocladorchiinae
      - Pseudocladorchis; Dadayius; Helostomatis; Nicollodiscus; Macrorchitrema; Microrchis; Travassosinia
    - Kalitrematinae
      - Kalitrema
  - Gastrodiscidae
    - Gastrodiscinae
      - Gastrodiscus; Homalogaster; Gastrodiscoides; Watsonius; Choerocotyle; Pseudodiscus
    - Brumptinae
      - Brumptia
  - Angiodictyidae
    - Angiodictyum; Denticauda; Deutobaris; Dictyangium; Hexangitrema; Hexangium; Microscaphidium; Parabaris; Octangium; Octangoides; Neoctangium; Polyangium; ?Pseudoparabaris
  - Gastrothylacidae
    - Gastrothylax; Fischoederius; Carmyerius; Johnsonitrema
  - Heronimidae
    - Heronimus
  - Mesometridae
    - Mesometra; Wardula; Centroderma

Yamaguti, 1971



As shown in the charts, opinion vary greatly respecting the scope and subdivision of the family. This is because these authors differ widely which characters to consider of family, subfamily or generic value. Furthermore, some systems were based not on extensive and critical examination of specimens but only on analysis of already published works.

Of the above systems, it appears that no single system in itself is entirely satisfactory. The system proposed by Yamaguti (1971) however is the most comprehensive and it will be followed to a large extent in this work. The ten genera and their synonyms in this study are therefore arranged as follows:

Paramphistomoidea

Paramphistomidae

Paramphistominae	Paramphistomum
	(Syn.: Liorchis, Srivastavaia)
	Calicophoron
	(Syn.: Bothriophoron)
	Gigantocotyle
	Explanatum
	Cotylophoron
Orthocoeliinae	Orthocoelium
	(Syn.: Ceylonocotyle, Cochinocotyle)
	Bilatorchis
	Leiperocotyle
Stephanopharynginae	Stephanopharynx
Balanorchiinae	Balanorchis
	(Syn.: Verdunia)

The family Paramphistomidae Fischoeder, 1901 is a large assemblage of species parasitizing almost all groups of vertebrates. Majority of those affecting mammals occurs in ruminants and has been the cause of fatal outbreaks among domestic ruminants. The disease caused by members of the group has been reviewed recently by Horak (1971).

It is already well documented that importation of animals as new stocks or for improving local stocks and exotic animals for Zoo display has resulted in the introduction and consequently establishment of some helminth parasites in new environments. Members of the family Paramphistomidae are no exception. Although their establishment in a new environment depends largely on the presence of suitable intermediate hosts and favourable climatic conditions, in areas where these factors are present, their establishment is insured. The species Calicophoron raja is common among domestic and wild ruminants in Africa south of the Sahara and it is known only in that continent. In this work however, examination of several specimens of amphistomes from cattle from various localities in Cuba sent to Dr. L.F. Khalil of the Commonwealth Institute of Helminthology by Dr. Prokopic showed C. raja to be the predominant species in the collection. It is possible that the species which is strictly African in distribution has been introduced to Cuba through importation of domestic stocks and because of the favourable climatic condition and the presence of a suitable intermediate host, has established itself in the island.

Importance of morphological and histological characters in the classification of paramphistomid trematodes

The classification of paramphistomid trematodes has been based largely on morphological and histological features. The value attached to these characters by various authors varied considerably which resulted in differences of opinion as to the composition and arrangement of species and genera within the family and status of some species. The characters employed are discussed below:

Morphological characters:

BODY SHAPE AND SIZE

The majority of the members of the family are conical in shape but others are dorso-ventrally flattened. In both forms however, the shape may be altered to some degree from short and broad to more elongate depending on the state of relaxation of the worm during fixation. As a consequence, the size of the body may also be altered. Näsmark (1937) has placed great emphasis on shape in distinguishing species of the genus Cotylophoron since he separated those forms exhibiting great breadth of body in relation to body length from those with long and conical body.

Some species have also been established and separated from closely allied ones mainly on body size. Buxifrons maxima Näsmark, 1937 and Stephanopharynx secundus Stunkard, 1929 are separable only from Buxifrons buxifrons (Leiper, 1910) and Stephanopharynx compactus Fischoeder, 1901 respectively because of their larger size. It has been demonstrated however that body size and therefore body length vary greatly even in the same species and

are affected by various factors like age and density of infection, site of attachment in the host, species of host and difference in the rate of growth even among species of the same age group. Horak (1967) has demonstrated experimentally that in Paramphistomum microbothrium, the worm grew larger and migrated more rapidly in cattle than in either sheep or goats. In cattle, the worms attached to the anterior ruminal pillar were larger than those attached to the posterior ruminal pillar while the reverse is true in sheep. Size also varied between light and heavy infections and the total body length showed the greatest range of variation. In the same species, Dinnik and Dinnik (1954) have also shown that specimens recovered from experimentally infected cattle and goats were much smaller in the latter than in the former. Crowding effect has also been observed to have a definite effect on the size of Zygocotyle lunatum, an amphistome of birds (Willey, 1941) and in two species of the related family Gastrothylacidae, Fischoederius elongatus and Gastrothylax crumenifer (Tandon, 1973).

Paramphistomids have the ability to extend and contract their bodies so that their length after fixation is determined by the state of relaxation during fixation and the kind of fixative used may also influence the degree of shrinkage. It is clear that size is influenced by several factors and therefore is not reliable. Shape on the other hand can be taken into account when fixation is satisfactory but there is a need of caution in attaching so much value to it.

SIZE OF ACETABULUM AND PHARYNX

The size of acetabulum and pharynx has been considered by Näsmark (1937), in combination with other characters, an important character at the generic level and has formed the basis of the erection of the genera Gigantocotyle and Macropharynx. Yamaguti (1958, 1971) has considered acetabular size of subgeneric value while accepting pharyngeal size of generic value. Horak (1967) has shown experimentally that in Paramphistomum microbothrium, while the total body length showed the greatest range of variation, acetabular measurement exhibited considerably smaller ranges of of variation. He concluded that acetabular measurement appears to be a more accurate indication of size than body length. The present study has also shown that the acetabulum is characteristically large and prominent in the genera Gigantocotyle and Explanatum and both are readily distinguished from other genera by this character. The acetabulum and pharynx are strong muscular organs and their rigidity makes tham stable structures which are least subject to deformation of the body as a result of contraction and relaxation of the specimens at the time of fixation. They can be employed as characters by indicating their sizes in relation to each other as ratio. Some authors however like Näsmark (1937), Gupta (1951), Gupta and Gupta (1970) and Lee and Lowe (1971) while taking their sizes into account have related them to that of the body length, a character already explained earlier as very variable. The histological feature of the acetabulum and pharynx has also been shown by Näsmark (1937) and subsequent authors as an important taxonomic feature and this is discussed under histological characters.

The presence or absence of pharyngeal pouches or diverticula is a very important taxonomic character at the generic level. The genera Stephanopharynx and Balanorchis are characterized by the presence of a single but large pharyngeal pouch and smaller but paired diverticles respectively. Both genera are readily separable from the majority of genera occurring in ruminants which are characterized by the absence of these structures.

THE OESOPHAGUS AND CAECA

The length of the oesophagus, although always given in species description, has no taxonomic value because of its ability to contract and extend. The muscular development of its wall and the lining of its internal surface are important features and these are discussed under histological characters.

The caeca in the paramphistomids, like the majority of digenetic trematodes consist of two blind tubes which run along the sides of the body. The nature and course of the caeca and the direction of their blind ends have been included by Fischoeder (1903) among the characteristics of several Paramphistomum species separated from P. cervi. Stiles and Goldberger (1910) has also employed them as one of the criteria in separating subgenera and species within the family. On the other hand, Maplestone (1923) and later Fukui (1929) maintained that both the degree and the point of termination of the caeca are variable within each species and that they cannot be used as reliable characters on which to separate species. Näsmark (1937) however has shown that the materials which Maplestone referred to as P. cervi actually consisted of several species, thus the different forms of caeca, but he did not include caecal features in his brief diagnosis

of species in the revision of the family. Several authors have shown that the convolution of the caeca and the direction of their blind ends are constant and characteristic features of the following species they have examined: Paramphistomum microbothrium Dinnik, 1954; Dinnik and Dinnik, 1954; Reinhardt, 1969 and Sey and Vishnyakov, 1976), P. sukari, P. phillerouxi and P. sukumum (Dinnik, 1954, 1961, 1964), P. daubneyi (Dinnik, 1962; Sey, 1974), Bilatorchis papillogenitalis and Leiperocotyle okapi (Eduardo, 1980a, 1980c).

The present study has also shown that in the majority of species examined, the character of the caeca is a useful diagnostic feature that could be used to support other features in specific identification.

THE ORGANS OF THE GENITAL SYSTEM

The arrangement of the genital organs in the body and their shapes and relative sizes are characters widely used not only in the family Paramphistomidae but also in other digenetic trematode families. Fukui (1929) claimed that the arrangement of the testes among amphistomes is more or less constant in a species and gave four types of testicular arrangements namely: tandem, side by side, obliquely tandem and dorso-ventrally oblique. Stiles and Goldberger (1910) have also utilized arrangement, position and size of the testes in relation to other organs in erecting new species and in their key to the species of the genus Paramphistomum. Mukherjee and Chauhan (1965) have also employed the same characters in separating species of the genus Ceylonocotyle. Prudhoe (1957) however has observed that the majority of the specimens of

Cotylophoron cotylophorum he examined has testes which are disposed in tandem but in very contracted ones they may be arranged diagonally. It was observed in this work that there are two distinct testicular arrangements among the species examined, tandem and horizontal. Tandem arrangement may vary from directly to obliquely (diagonal by some authors) tandem while horizontal may become slightly oblique when specimens become distorted due to poor fixation. In either case, it is very important to examine several specimens to be able to determine the normal testicular arrangement and any slight deviation should be interpreted as variation due to fixation and other factors. The presence or absence of lobulation in the testes is an important feature among species in this group. Majority of the species occurring in ruminants has lobed testes but some like Paramphistomum liorchis and Balanorchis anastrophus have unlobed testes. Dinnik (1954, 1961, 1962, 1964) has attempted to count the number of testicular lobes by including it in describing his species. The writer has also tried to count the number of testicular lobes in specimens examined here but it seems impractical. It is very difficult to accurately count the number of lobes because of the size and thickness of the worms. In sections, it is more difficult to follow where lobulation starts and where it ends. In view of this, lobulation can only be expressed as deep or strong, shallow or just indented.

The development of the pars musculosa is already an established character of generic importance in combination with other features. Fischoeder (1902, 1903) first employed it by subdividing species of the genus Paramphistomum into groups. Yamaguti (1971) and

Eduardo (1980c) employed it in separating genera of the subfamily Orthocoeliinae and also in the present work of the subfamily Paramphistominae. The presence or absence of a cirrus pouch is also an important taxonomic character. Within the scope of this work, only the genus Balanorchis is characterized by a cirrus pouch.

The position of the ovary in relation to the testes when in combination with other characters is an important feature in some genera. The majority of the genera examined here have ovaries and Mehlis' glands which lie posterior to the testes but in the genera Bilatorchis and Balanorchis, these organs are in between the two testes which are horizontal and far apart. In the related family Gastrothylacidae, the genera Carmyerius and Gastrothylax are separable from Fischoederius by the same kind of testes/ovary and Mehlis' gland arrangement. The size of the ovary in relation to the testes in all species examined here is consistently smaller except in only one species, Cotylophoron bareilliense where the reverse is true. The extent and shape of the vitelline follicles have been included in previous descriptions of amphistome species but one aspect has been overlooked, i.e. whether the vitellaria are confluent or not. The present work has shown that this character is of specific value and could be used to separate some species in a genus. Vitellaria may either be confluent or not. If confluent, it is either only anteriorly (Paramphistomum ichikawai, P. hiberniae) or only posteriorly (Gigantocotyle gigantocotyle, G. symmeri, Leiperocotyle congolense) or both (Cotylophoron panamensis). The presence or absence of Laurer's canal crossing the excretory vesicle or duct is already a recognised

character at the subfamily level and it is employed to separate the Paramphistominae and Orthocoeliinae.

The exact position of the genital pore on the ventral surface in relation to the upper parts of the digestive tract, i.e. pharynx, oesophagus and its bifurcation has been utilized by some authors in separating species. The genital pore however varies in position at various points in this region depending on the degree of contraction or relaxation during fixation. The presence of a genital sucker in combination with other characters is an important feature of some genera and has formed the basis of the erection of the genera Cotylophoron and Leiperocotyle.

TEGUMENTAL PAPILLAE

Some previous authors have observed and included in their description of some paramphistomid species the occurrence of tegumental papillae but their value in taxonomy has never been seriously considered. Fukui (1929) first pointed out the value of these structures in the identification of species in the group. He maintained that in the Paramphistominae, small papillae are almost always present especially around the oral aperture and their distribution differs in different species. These papillae are relatively large in Paramphistomum gotoi and P. explanatum. Other authors have also observed the presence of tegumental papillae either around the oral end or on the wall of the genital atrium in some species of paramphistomids they have examined, among them are Fischoeder (1903), Stiles and Goldberger (1910), Leiper (1910), Dollfus (1950), Dinnik (1961, 1962, 1964) and Velazquez-Maldonado (1976). In all the above however, observation

was made under light microscopy, hence the exact nature and type of papillae present were not established.

The use in recent years of scanning electron microscopy in describing surface topography of helminth parasites has become increasingly useful. Many species of other digenetic trematodes have been examined by this method. In the superfamily Paramphistomoidea however, as far as the writer is aware, only four species have been examined by this method, Megalodiscus temperatus (Morris, 1973; Nollen and Nadakavukaren, 1974), Bilatorchis papillogenitalis, Orthocoelium indonesiense and Leiperocotyle okapi (Eduardo, 1980a, 1980b, 1980c).

The enormous collection of amphistomes at the writer's disposal has afforded the opportunity to examine many species where sufficient number and suitable material were available under the scanning electron microscope. The results are discussed below and the microphotographs accompany the description of each species in the systematic section of this work.

Majority of the species examined by the above method revealed the presence of surface structures which are termed here tegumental papillae. It has been observed that the occurrence, distribution and type of these tegumental papillae appear to be consistent in the same species even in specimens from various hosts and localities and of different ages. Many species examined here were from various hosts and localities. In addition, among the numerous specimens of Calicophoron microbothrium were two lots, each was of a different age (124 days and three years old) and both were recovered experimentally (Dr. J.A. Dinnik's feeding experiment). In all the above material, each species even from various sources revealed

consistently the same type and distribution pattern of tegumental papillae. Tegumental papillae when present were observed to occur on four different areas of the body namely, around the oral opening, around the genital pore region, on the wall of the genital atrium and around the acetabular opening. They occur either only on a single area or on various possible combinations of the four areas. It was also observed that the papillae around the acetabular opening are always fewer, smaller and randomly arranged. Those on the wall of the genital atrium are larger and very closely packed. Those around the genital pore region usually are extension of those around the oral opening and therefore are of the same type and size as the latter. However, in Calicophoron microbothrioides, C. sukari and Stephanopharynx compactus, those around the genital pore region are distinctly much larger than those around the oral opening while the reverse is true in Calicophoron raja. The papillae around the oral opening proved very interesting. They varied in form and structure among different species but appeared to be consistent among specimens of the same species. Six types of papillae on this region were observed and only one type occurred in a particular species. The six types are as follows and are illustrated in the accompanying microphotographs (Figs. 1-3): a) Dome to conical non-ciliated papilla; b) Dome to conical ciliated papilla; c) Short and stumpy papilla covered with hair-like processes; d) Long non-branching and non-ciliated papilla; e) Long papilla with simple uniciliated branches; and f) Long papilla with bulb-like multiciliated branches. The first type is the most common and was observed in the majority of species examined.

The occurrence of the above types of anterior papillae among the different species examined including those non-ruminant forms not treated in the systematic part is given in the accompanying list. As shown above, tegumental papillae (their occurrence, distribution and type) appear to have some taxonomic value and can be employed to support other characters in the specific identification of some mammalian amphistomes.

Types of anterior papillae and their occurrence among the different species examined

a). Dome to conical non-ciliated papilla

Calicophoron calicophorum
C. clavula
C. daubneyi
C. microbothrium
C. microbothrioides
C. phillerouxi
C. raja
C. sukari
C. sukumum
Cotylophoron cotylophorum
C. panamensis
Gigantocotyle symmeri
Orthocoelium dinniki n.sp.
O. gigantopharynx
O. indonesiense
O. scoliocoelium
Paramphistomum epiclitum
P. gotoi
P. hiberniae
P. ichikawai
P. leydeni
P. liorchis
Stephanopharynx compactus

b). Dome to conical ciliated papilla

Bilatorchis papillogenitalis
Cotylophoron bareilliense
Glyptamphistoma paradoxum
Leiperocotyle gretillati

c). Short and stumpy papilla covered with hair-like processes

Leiperocotyle okapi
Orthocoelium dicranocoelium
Paramphistomum gracile

d). Long non-branching and non-ciliated papilla

Hawkesius hawkesi

e). Long papilla with simple uniciliated branches

Balanorchis anastrophus

f). Long papilla with bulb-like multiciliated branches

Nilocotyle sp.
Platyamphistoma polycladiforme
Sellsitrema sellsi

g). Anterior papilla absent

Cotylophoron macrosphinctris

Gigantocotyle duplicitestorum

G. gigantocotyle

Paramphistomum cervi

P. cephalophi n.sp.

FIGURE 1

Types of anterior papillae (i)

Dome to conical non-ciliated papilla (a-f)

a,c,e - General view of oral opening

b,d,f - Corresponding closer view of papillae

Scale bar value:

a - 200 µm; b - 20 µm; c - 100 µm; d - 10 µm:

e - 100 µm; f - 50 µm

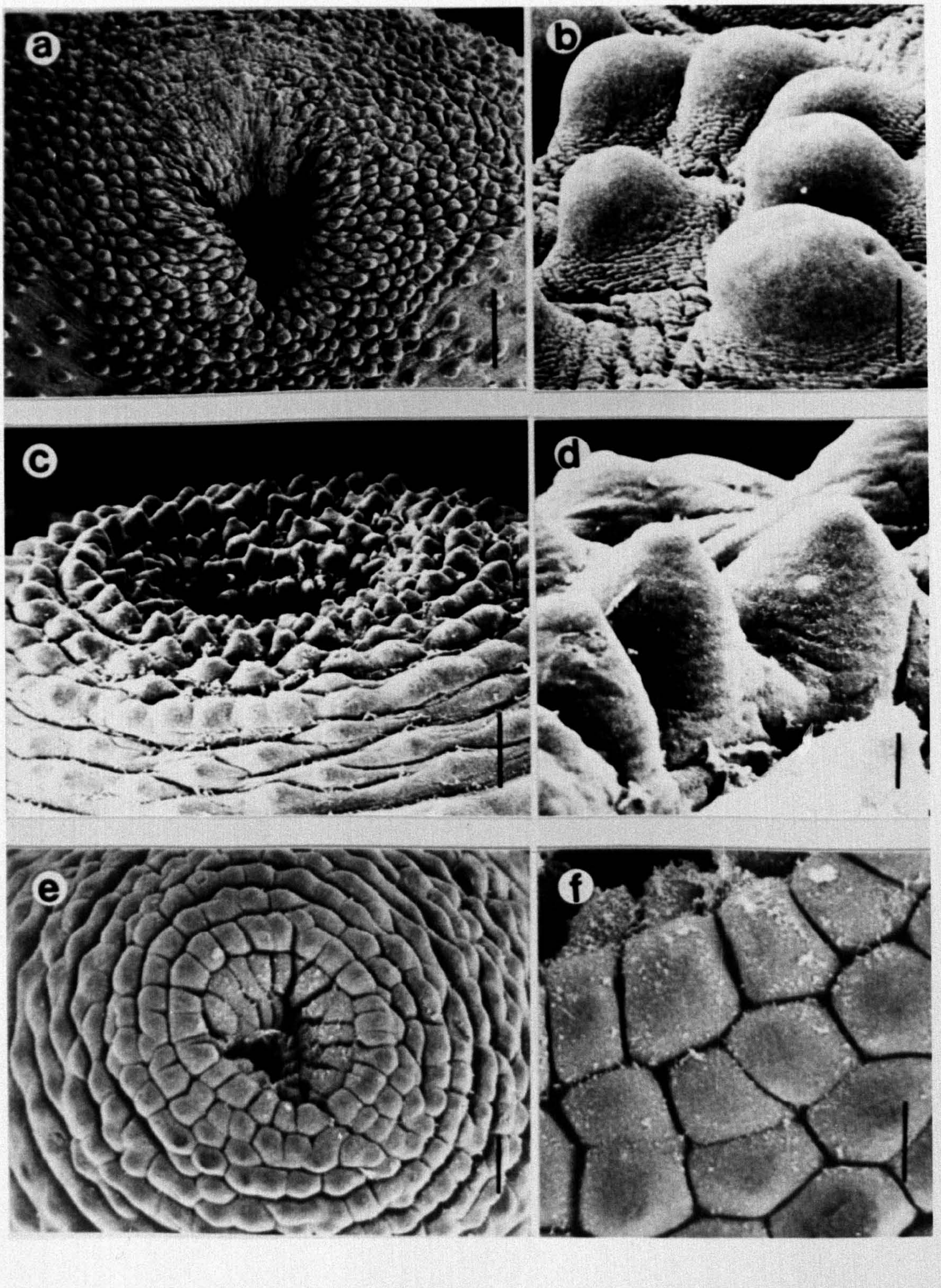

a
b
c
d
e
f

FIGURE 2

Types of anterior papillae (ii)

a-b, Dome to conical ciliated papilla

c-d. Short and stumpy papilla covered with hair-like processes

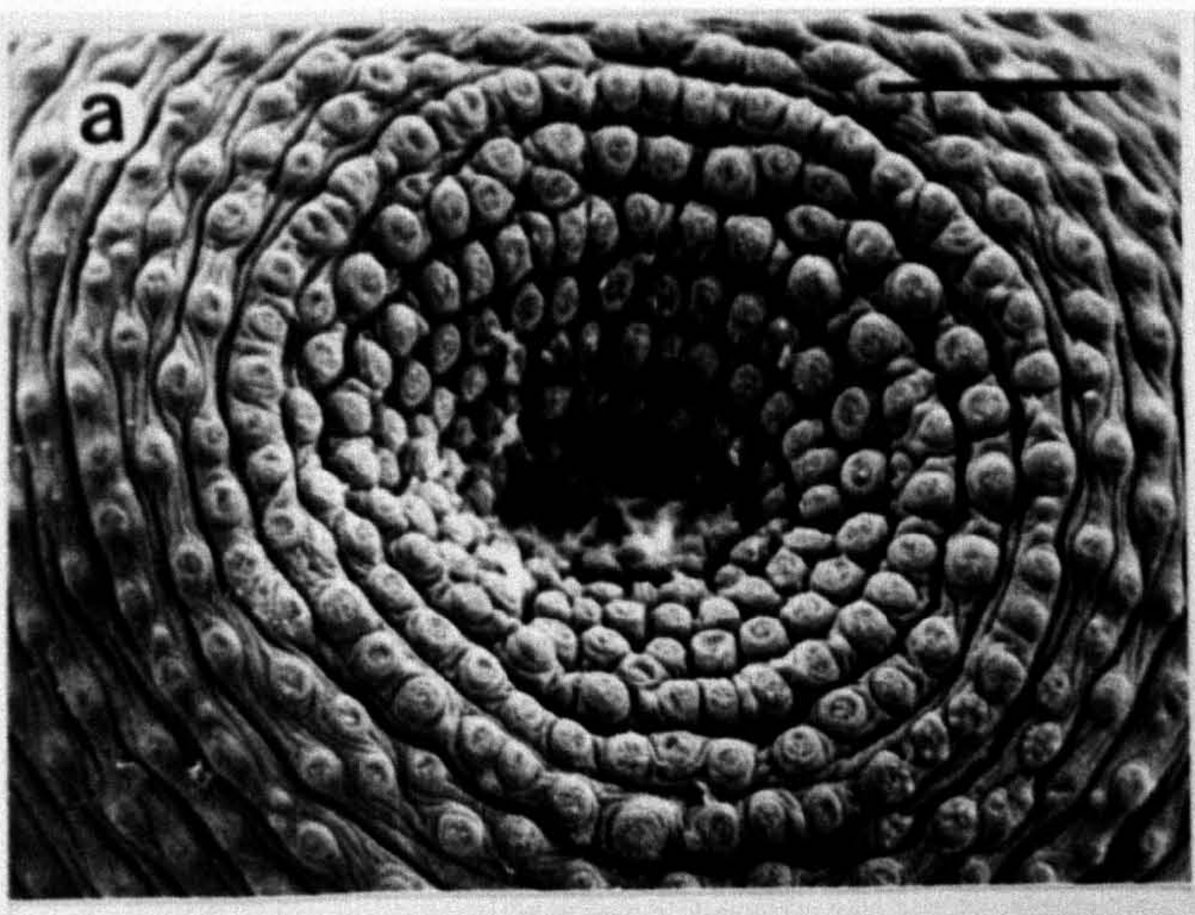
e-f. Long non-branching and non-ciliated papilla

a,c,e - General view of oral opening

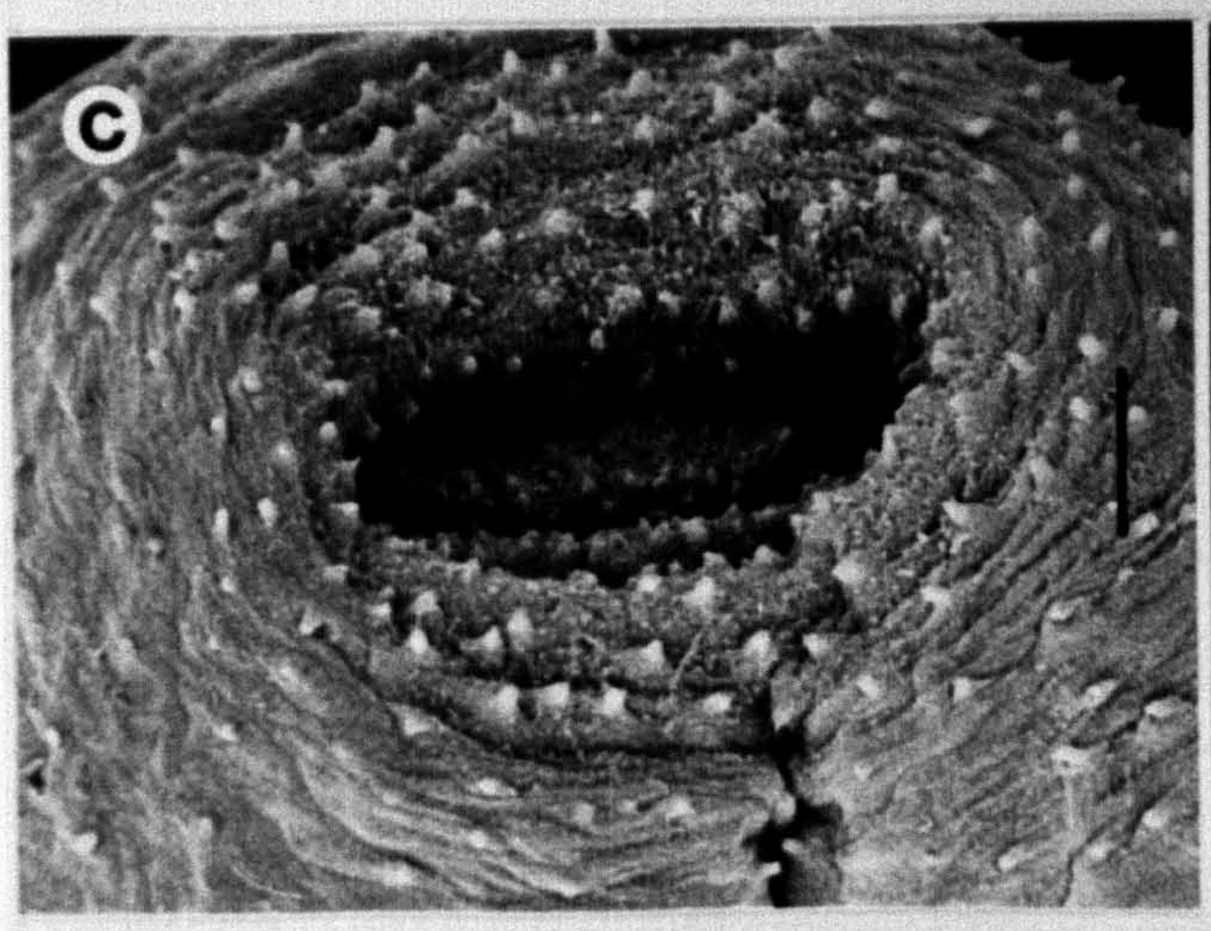
b,d,f - Corresponding closer view of papillae

Scale bar value:

a - 50 µm; b - 10 µm; c - 50 µm; d - 20 µm;
e - 50 µm; f - 10 µm


a


b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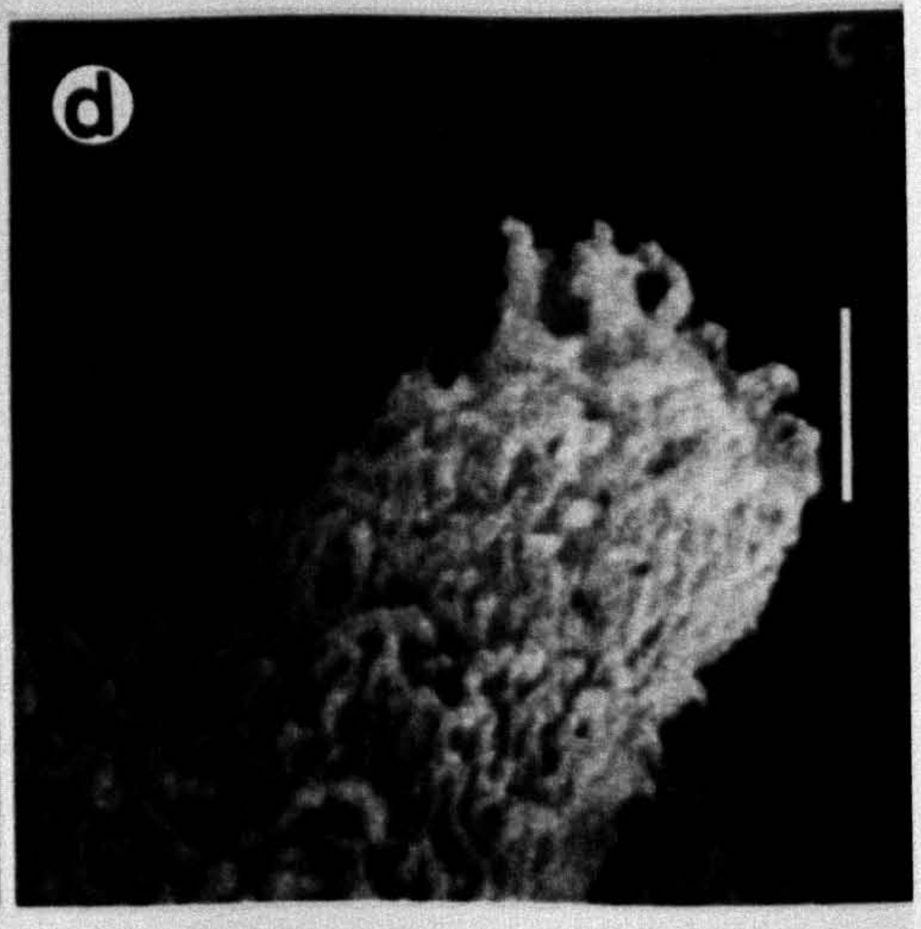
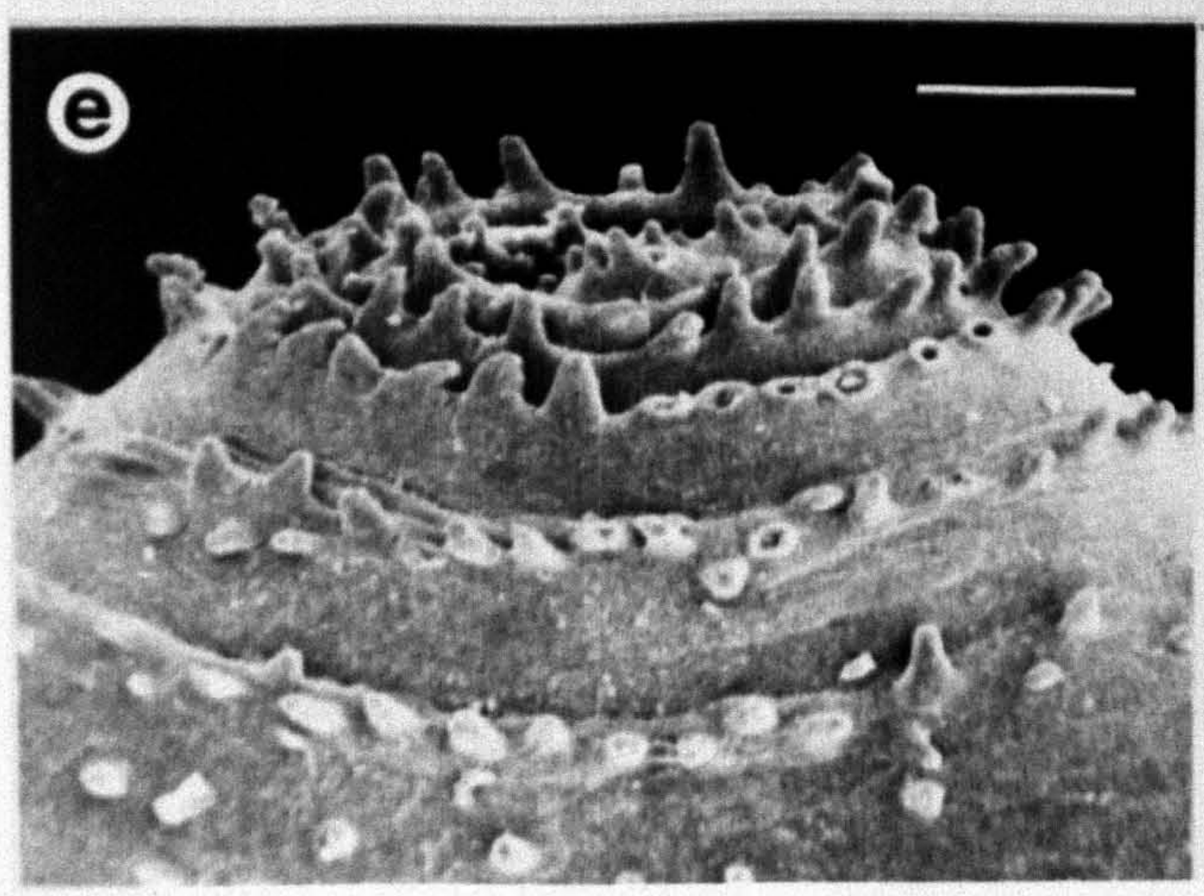

d


e

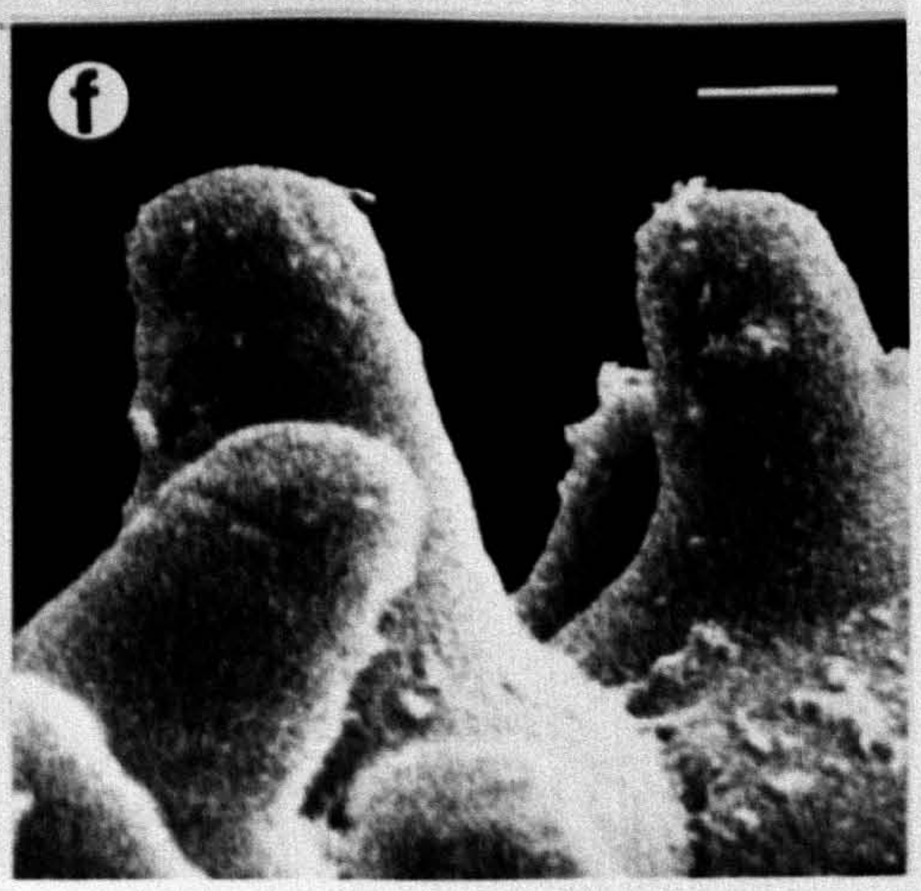

f

FIGURE 3

Types of anterior papillae (iii)

a-b. Long papilla with simple unicilated branches

c-f. Long papilla with bulb-like multiciliated branches

a,c,e - General view of oral opening

b,d,f - Corresponding closer view of papillae

Scale bar value:

a - 50 µm; b - 10 µm; c - 50 µm; d - 5 µm;

e - 50 µm; f - 1 µm

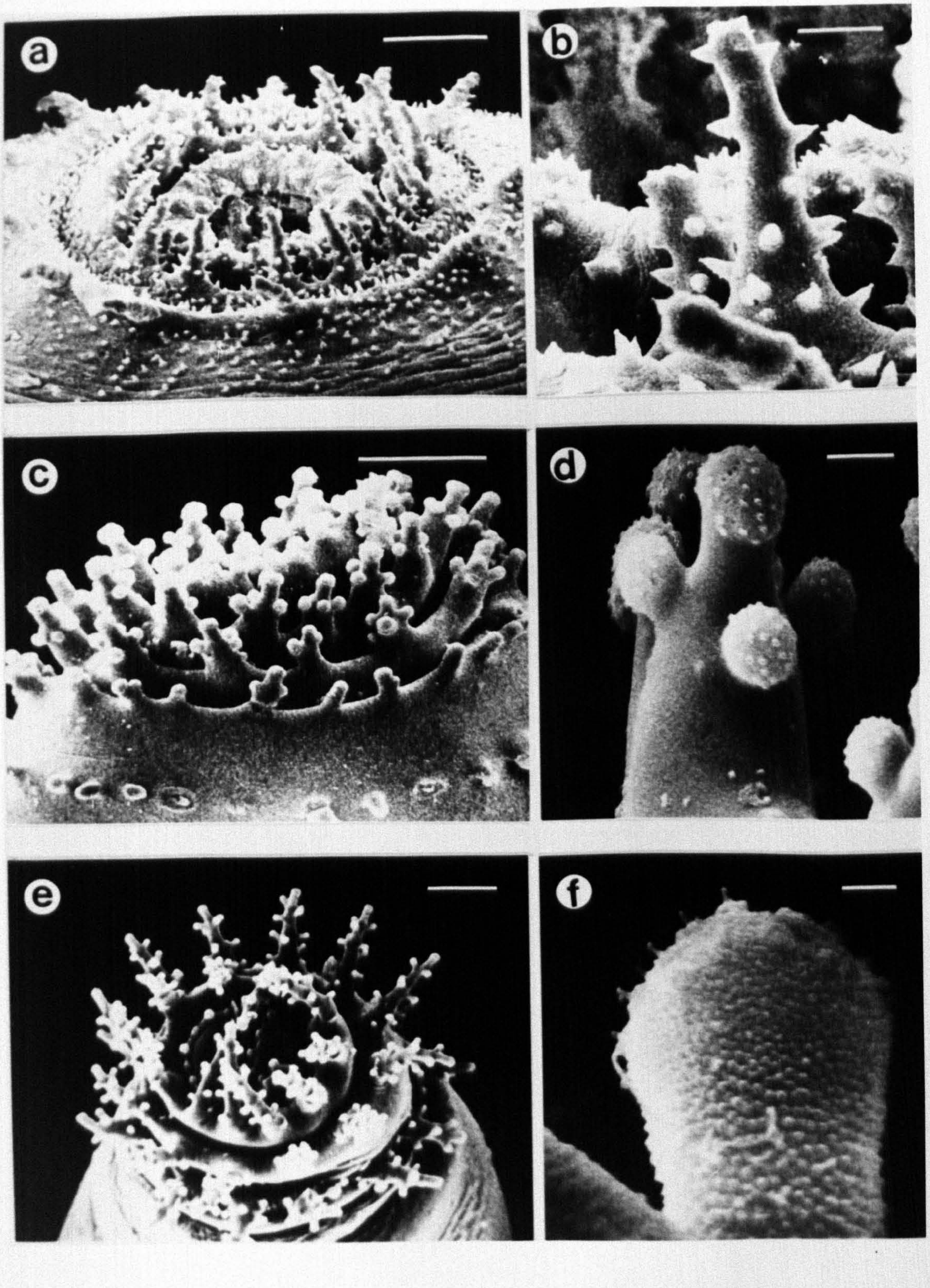

a
b
c
d
e
f

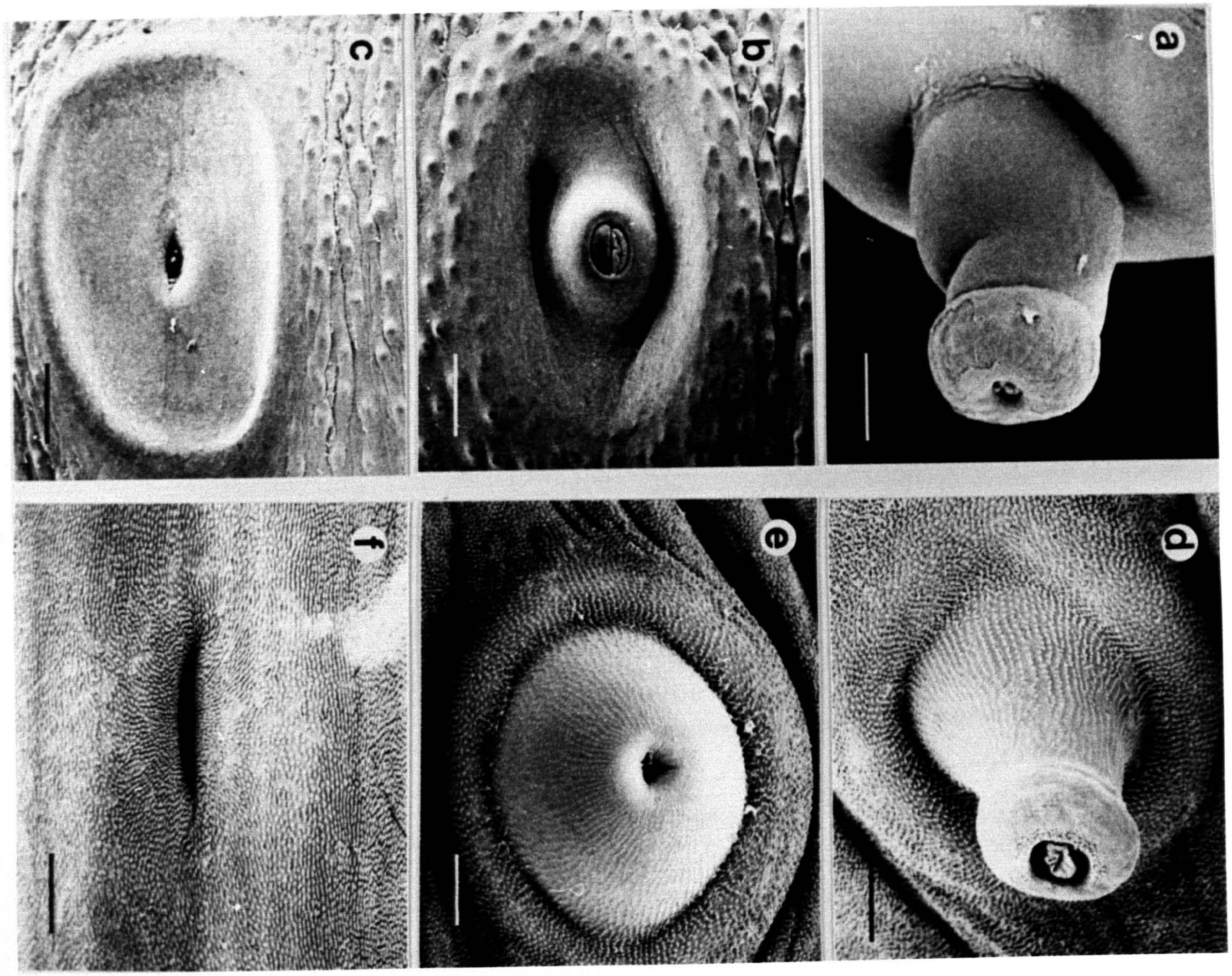
FIGURE 4

Comparison of the tegumental surface of the genital pillar of Calicophoron calicophorum (a-c) and C. raja (d-f) at various degrees of extension and contraction. Note the presence of small papillae densely arranged on the genital pillar of the latter species which are lacking on the former species. The large papillae on the area at a distance surrounding the genital pore region of C. calicophorum are extension of those occurring around the oral end.

Scale bar value:

a - 100 µm; b - 200 µm; c - 200 µm; d - 100 µm;

e - 100 µm; f - 100 µm


a
b
c
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e
f

FIGURE 5

Some examples of closely related species showing differences in the occurrence and type of anterior papillae.

a. Paramphistomum cervi (scale bar = 100 µm)

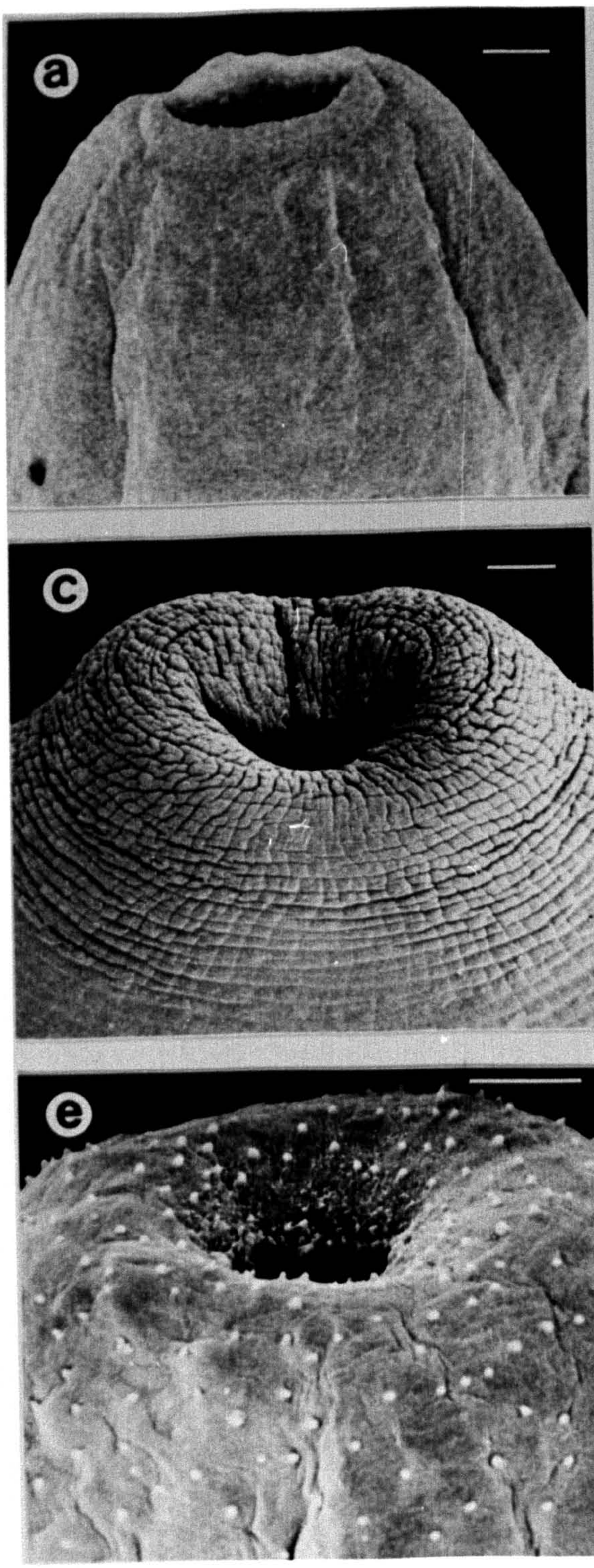
b. P. leydeni (scale bar = 100 µm)

c. Gigantocotyle duplicitestorum (scale bar = 100 µm)

d. G. symmeri (scale bar = 200 µm)

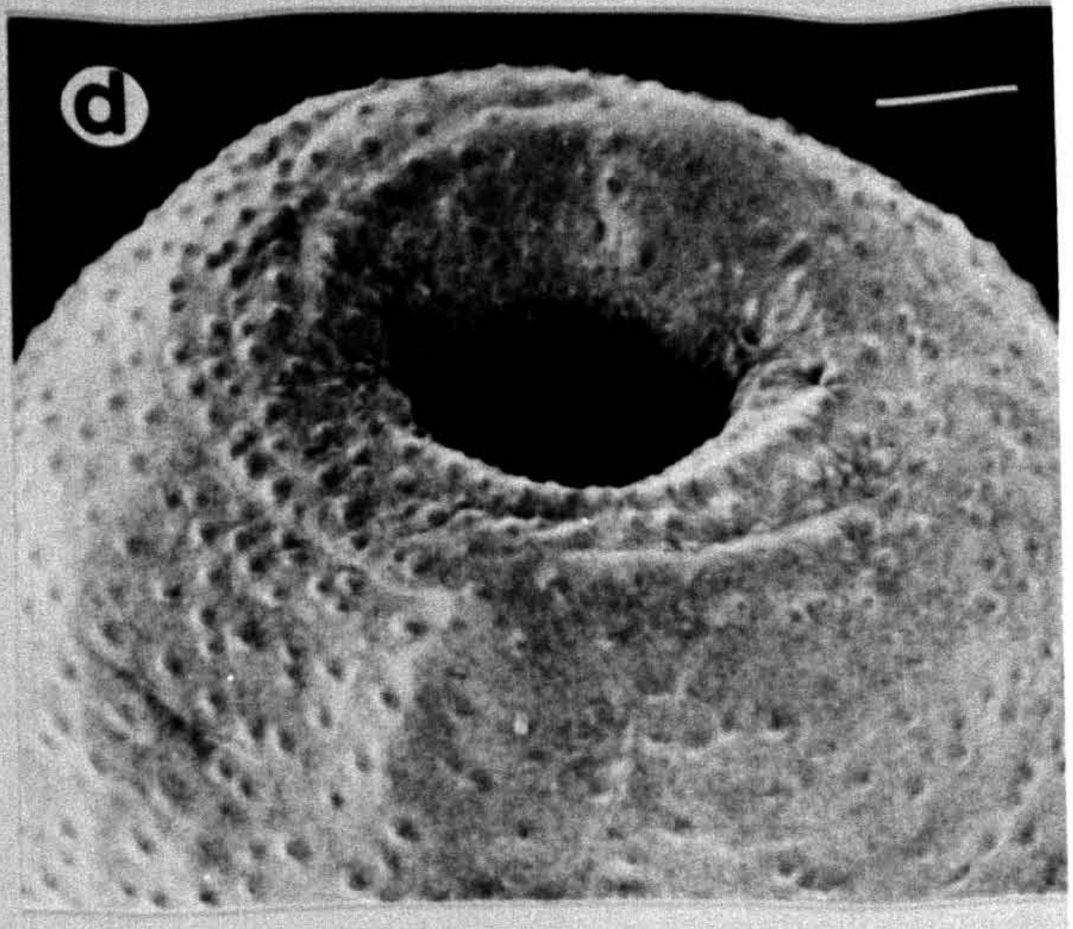
e. Orthocoelium dicranocoelium (scale bar = 150 µm)

f. O. scoliocoelium (scale bar = 150 µm)

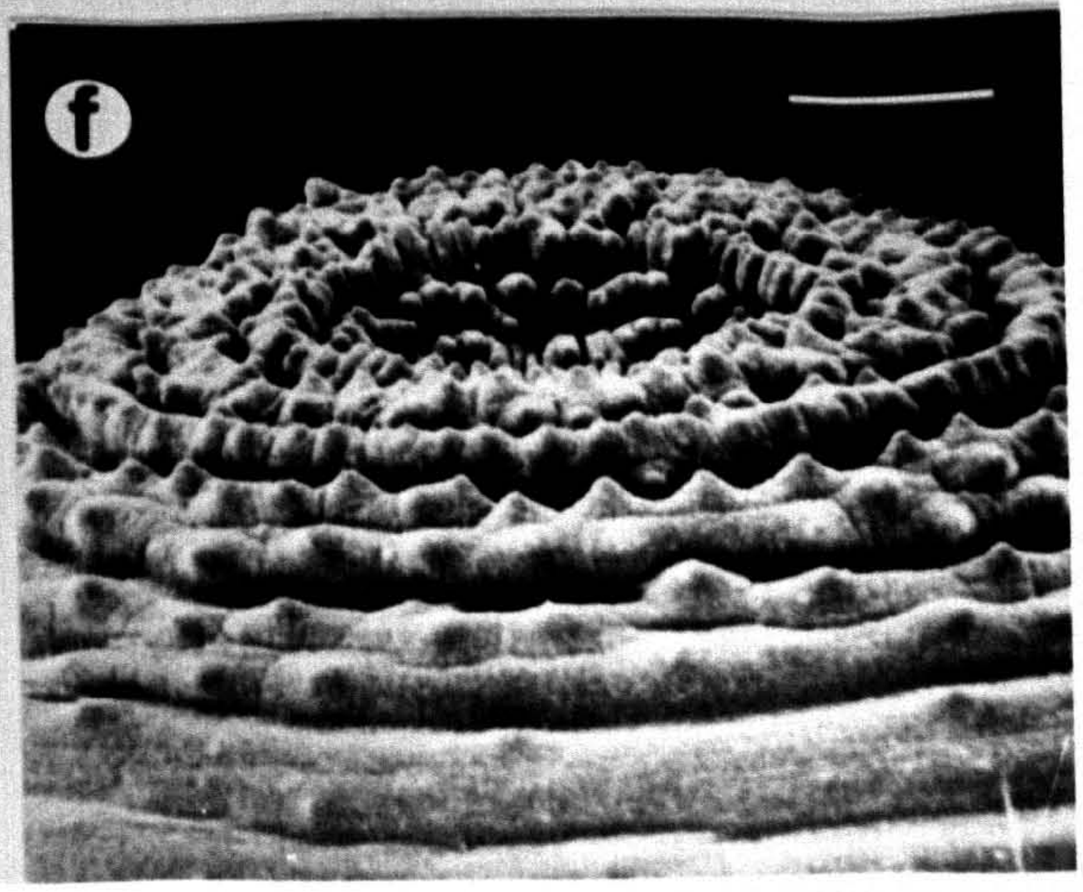

a


b

c


d

e


f

Histological characters:

Näsmark (1937) has introduced a new basis of classification of the Paramphistomidae which involves the study of the histological structure of the acetabulum, pharynx and terminal genitalium as seen in median section. The idea however was first initiated by Fukui (1929) in his revision of the Japanese amphistomes. By this method, Näsmark was able to confirm validity of the species of Fischoeder (1901, 1902, 1903, 1904) which were synonymized by Maplestone (1923) and new genera and species were also established as a result. On this basis, he classified the acetabulum, pharynx and terminal genitalium of the species available at that time into different structural types. The system has attracted criticism from Prudhoe (1957) but subsequent authors and also this study have shown that the system is very useful for this group of trematodes. It should be noted however that Näsmark's work is not entirely without error or deficiency, as will be pointed later in this section.

THE ACETABULUM

The different types of acetabulum established by Näsmark (1937) were based on the different arrangement of the musculature particularly the series of circular muscle units as seen in median sagittal section. He mentioned four series of circular muscle units, two series in the dorsal half (dorsal exterior and dorsal interior) and two in the ventral half (ventral exterior and ventral interior). These and other details were illustrated in a schematic representation of a general type of acetabulum in median sagittal section with all the parts necessary for diagnosis. However,

there is another series of circular muscle units which was not taken into account by Näsmark. The units of this series lie along the exterior wall in the area between the dorsal exterior and ventral exterior series. Näsmark made no mention of this series of units but his illustration of Paramphistomum cervi (Fig. 90), Calicophoron ijimai (Figs. 11 & 93) and Cotylophoron jacksoni (Fig. 95) reveal their presence. Gupta and Dutta (1967) noted the same series of muscle units in their material of Gastrothylax crumenifer of the related family Gastrothylacidae and called the units "dome units". Reinhardt (1969) observed the same units in his specimens of Paramphistomum microbothrium and gave the term "median exterior circular series". In this study, it was observed that all of the species here examined with the exception of Gigantocotyle duplicitestorum revealed the presence of these units. Other authors may probably have observed these units but ignored them since these were not mentioned in Näsmark's work. The term median exterior circular series as proposed by Reinhardt (1969) seems appropriate for this particular series and therefore is adapted in this work.

Nasmärk (1937) regarded the type of acetabulum a character of generic value and used this as one of the characters of the genera Paramphistomum, Calicophoron and Ceylonocotyle (now Orthocoelium). However, he himself has shown that species of the genus Gigantocotyle have different types of acetabulum. It was observed in the present study that contrary to Näsmark's description, the acetabulum of Calicophoron raja differs from the rest of the species assigned by him in the genus because of the presence of a second group of units in the dorsal exterior series.

Recently described species like Orthocoelium indonesiense (Eduardo, 1980b) and Cotylophoron xiangjiangense (Wang, 1979) possess also an acetabular type different from other members in their respective genera. It appears therefore that histological feature of the acetabulum is only of value at the species level and that it could not be employed as a generic character.

It should also be mentioned here that Näsmark (1937) has referred the acetabulum of Gigantocotyle gigantocotyle to the explanatum type but specimens examined here revealed that it is not of that type because of the presence of a second group of small and few circular muscle units in the ventral exterior circular series. This is clearly illustrated in figure 6. Because of this, the acetabulum in question differs from all known types and it is defined and illustrated below as the gigantocotyle type (new type).

The different types of acetabulum observed among the different species examined in this work are listed, defined and illustrated below. These include both new and already known types. A schema-representation of a general type of acetabulum as seen in median sagittal section modified from Näsmark (1937) and showing all the different features for diagnosis is also provided (Fig. 7). Terminology is that of Näsmark (1937) plus additional terms already discussed earlier.

FIGURE 6

Gigantocotyle gigantocotyle (Brandes in Otto, 1896)

Näsmark, 1937

The dorsal (a) and ventral (b) parts of the acetabulum as seen in median sagittal section showing that in both, the exterior circular series has a second group of circular muscle units as indicated by arrows (scale bar = 185 µm).

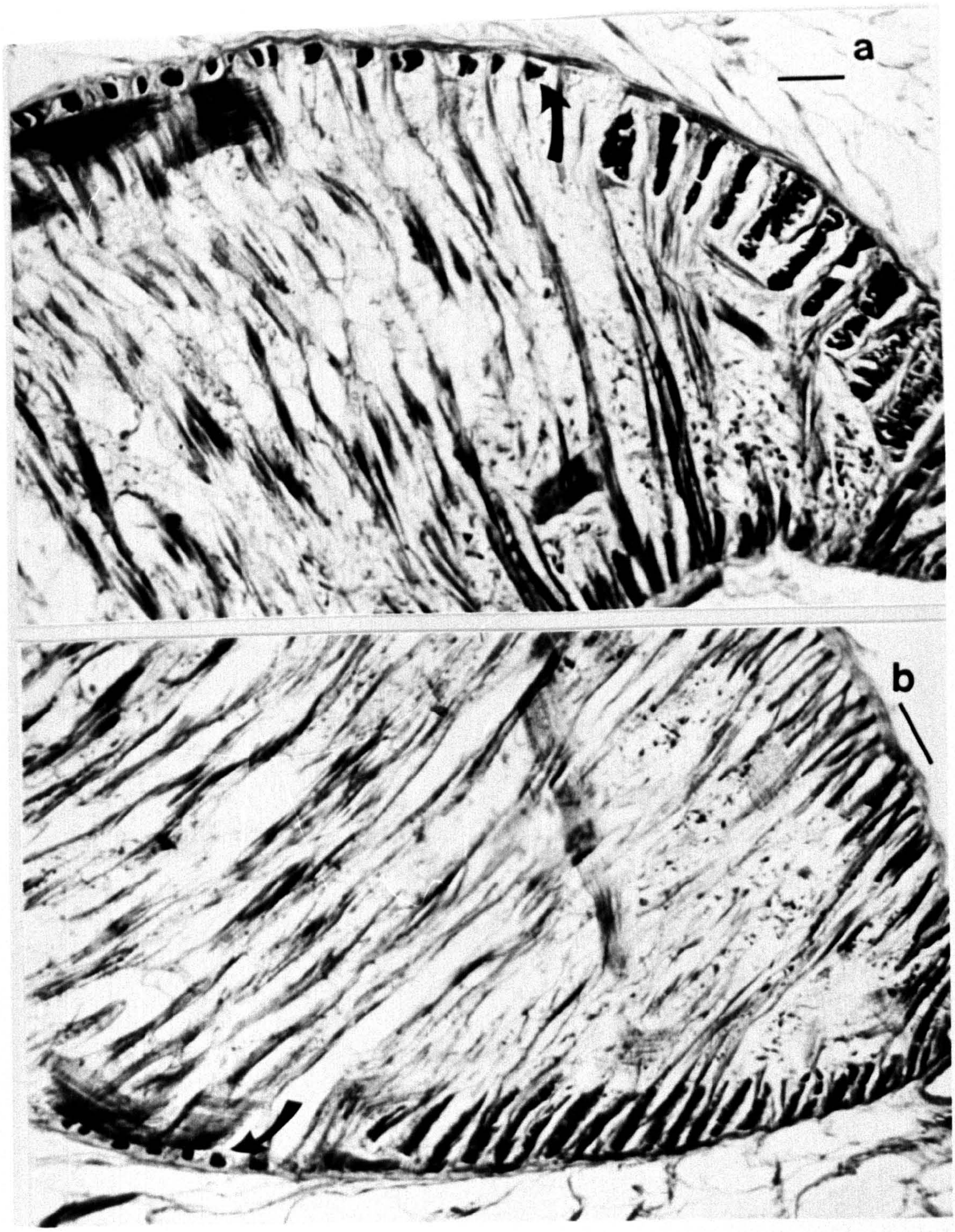

a
b

FIGURE 7

A schematic representation of a general type of acetabulum as seen in median sagittal section showing details which are necessary for diagnosis (modified from Näsmark, 1937).

Key to abbreviations:

dec - dorsal exterior circular muscle series

dec_1 - dorsal exterior circular muscle series, group one

dec_2 - dorsal exterior circular muscle series, group two

dic - dorsal exterior circular muscle series

el - exterior longitudinal muscle fibres

mec - median circular muscle series

of - oblique muscle fibres

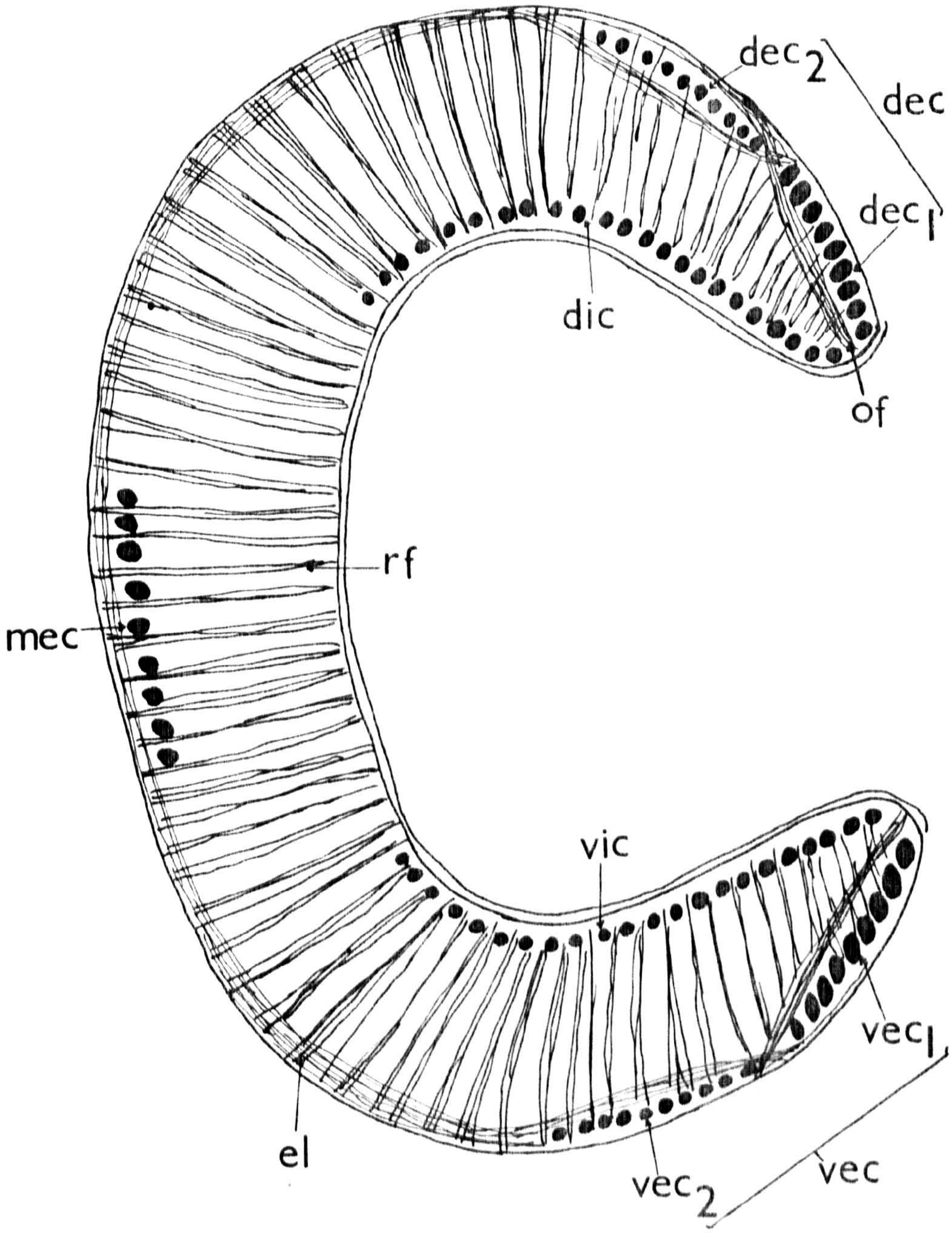
rf - radial muscle fibres

vec - ventral exterior circular muscle series

vec_1 - ventral exterior circular muscle series, group one

vec_2 - ventral exterior circular muscle series, group two

vic - ventral interior circular muscle series


dec2
dec
dec1
dic
of
rf
mec
vic
vec1
el
vec2
vec

Types of acetabulum observed among the different species examined in this work

1. Gigantocotyle type (new type), Fig. 8a

Size enormous. Characterized by the dorsal and ventral exterior circular series both having two groups of units, d.e.c.1, d.e.c.2 and v.e.c.1, v.e.c.2 respectively. Both the d.e.c.1 and v.e.c.1 units are relatively well developed. Both the d.e.c.2 and v.e.c.2 units are much smaller in size but the former are much greater in number than the d.e.c.1 units while the latter are much fewer in number than the v.e.c.1 units. The units of the dorsal and ventral interior circular (d.i.c. and v.i.c.) series are moderately developed and gradually diminish in size towards the interior of the series. Median exterior circular (m.e.c.) series consists of irregularly spaced units. Radial fibres well developed; oblique fibres few and weakly developed; exterior longitudinal fibres distinct.

2. Explanatum type (Näsmark, 1937), Fig. 8b

Size enormous. The d.e.c. series also consists of two groups of units but the v.e.c. series consists only of a single group. The d.e.c.1 and v.e.c. units are strongly developed, the d.e.c.2 units are much smaller but greater in number than the d.e.c.1 units. The units in the d.i.c. and v.i.c series are moderately developed diminishing in size towards the interior of the series. M.e.c. series consists of irregularly spaced units. Radial fibres well developed; oblique fibres few and weakly developed; exterior longitudinal fibres distinct.

FIGURE 8

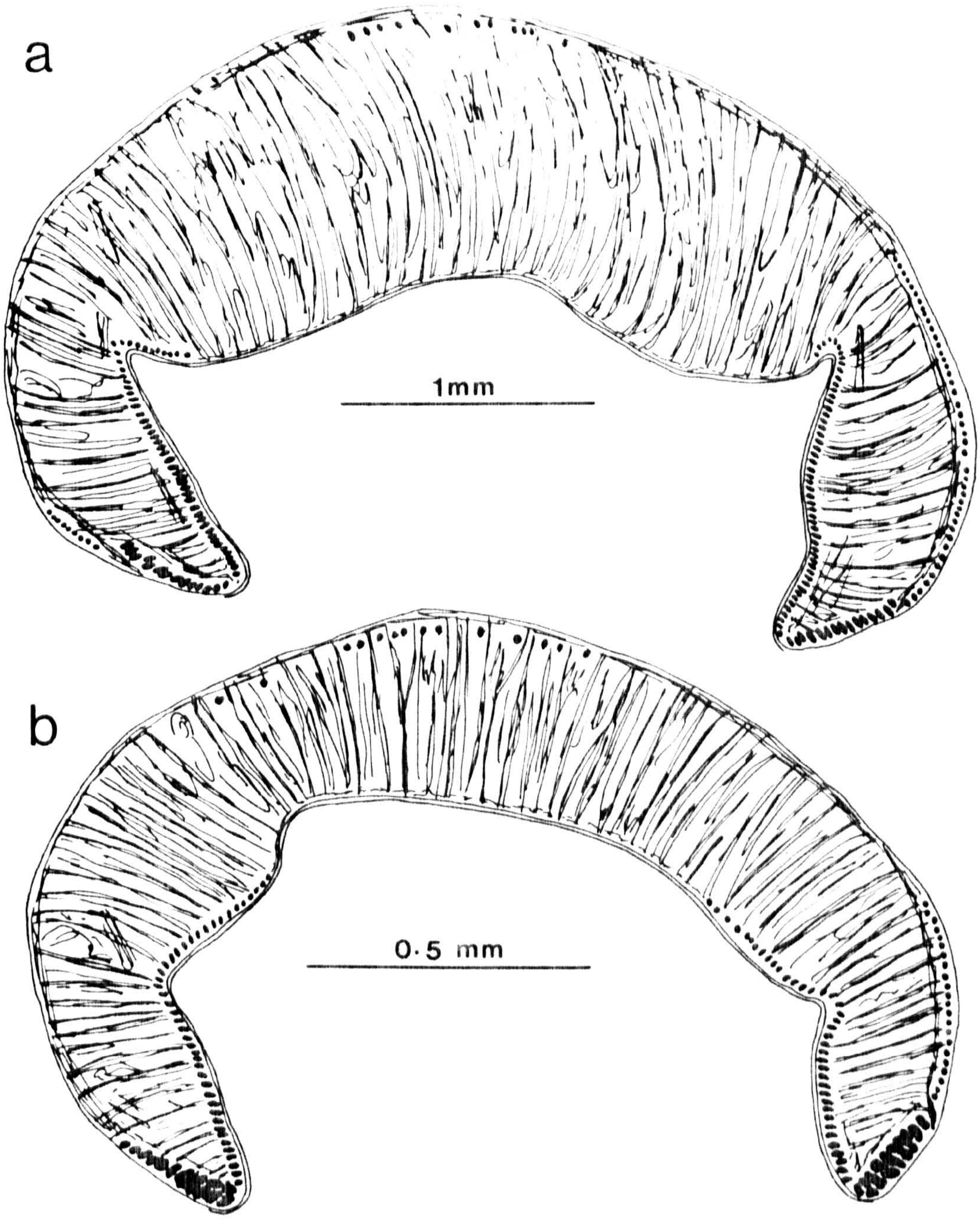
Types of acetabulum (i)

(median sagittal section)

a. Gigantocotyle type (new type)

b. Explanatum type (Näsmark, 1937)

a



b

3. Symmeri type (Näsmark, 1937), Fig. 9a

Size enormous. The d.e.c. series consists of two groups of units, the d.e.c.2 units are smaller in size, fewer in number and irregularly spaced than the d.e.c.1 units. The d.i.c. and v.i.c. units are fairly developed. The v.e.c. series consists only of a single group of units. The m.e.c. series consists of irregularly spaced units. Radial fibres well developed; oblique fibres few and weakly developed; exterior longitudinal fibres distinct.

4. Duplicitestorum type (Näsmark, 1937), Fig. 9b

Size enormous but thickness of wall is relatively narrow. Like the preceeding type, the d.e.c. series also consists of two groups of units but the d.e.c.2 units are larger in size and usually greater in number than the d.e.c.1 units. The latter in this case are much smaller and sometimes weakly developed. The d.i.c and v.i.c. series consist of small units. The m.e.c. series is absent. Radial fibres very well developed; oblique fibres very few and sometimes insignificant; exterior longitudinal fibres distinct.

5. Paramphistomum type (Näsmark, 1937), Fig. 10a

Moderate in size. The d.e.c. series consists of two groups of units, the d.e.c.1 units are well developed but not as strongly developed as that of the explanatum type, the d.e.c.2 units are much smaller in size but greater in number than the d.e.c.1. units. The v.e.c. series consists only of a single group of units. The d.i.c. and v.i.c. units are well developed but diminish in size towards the interior of the series. The m.e.c. series consists of irregularly spaced units. Radial fibres fairly developed; oblique

FIGURE 9

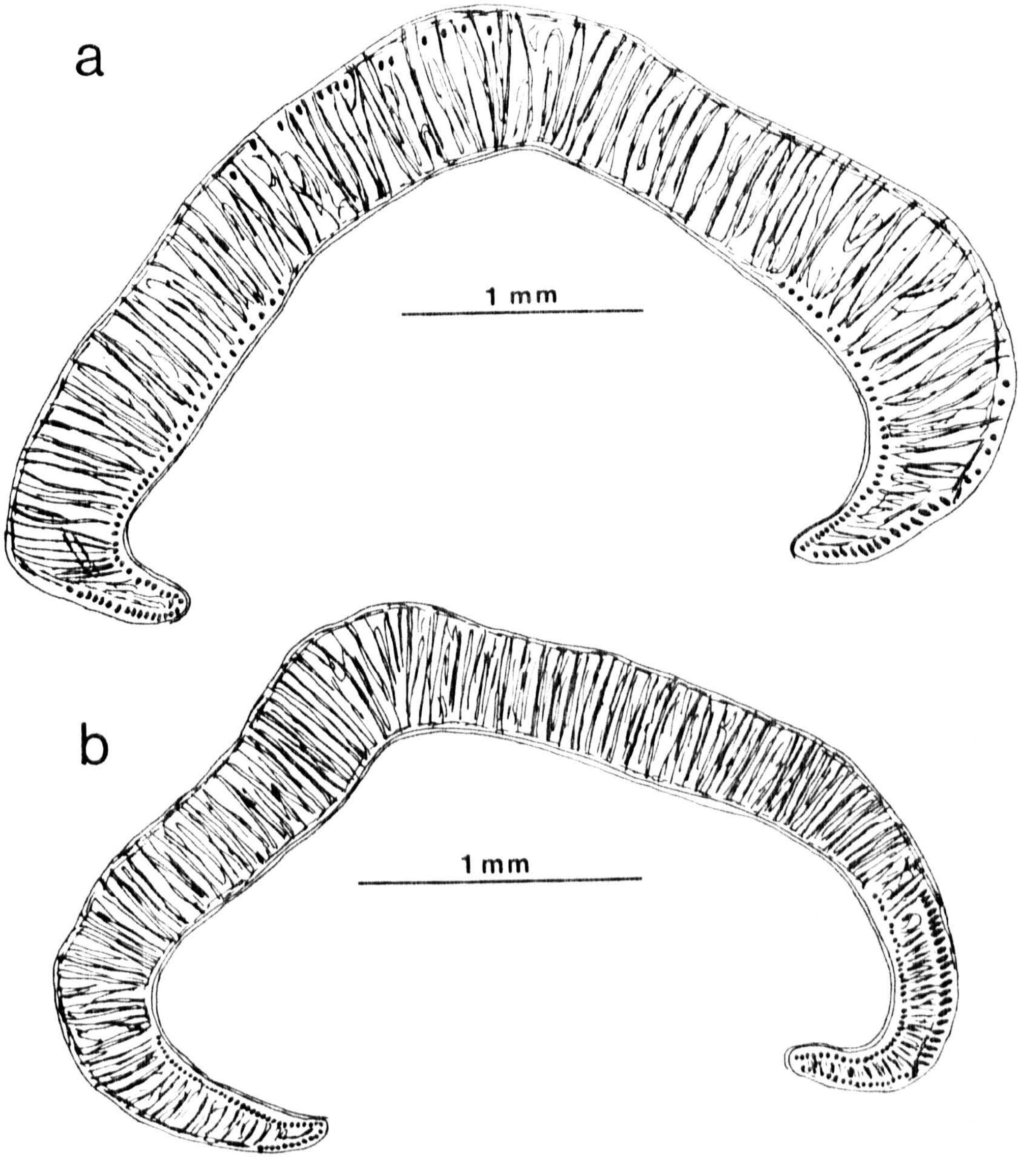
Types of acetabulum (ii)

(median sagittal section)

a. Symmeri type (Näsmark, 1937)

b. Duplicitestorum type (Näsmark, 1937)

a



b

FIGURE 10

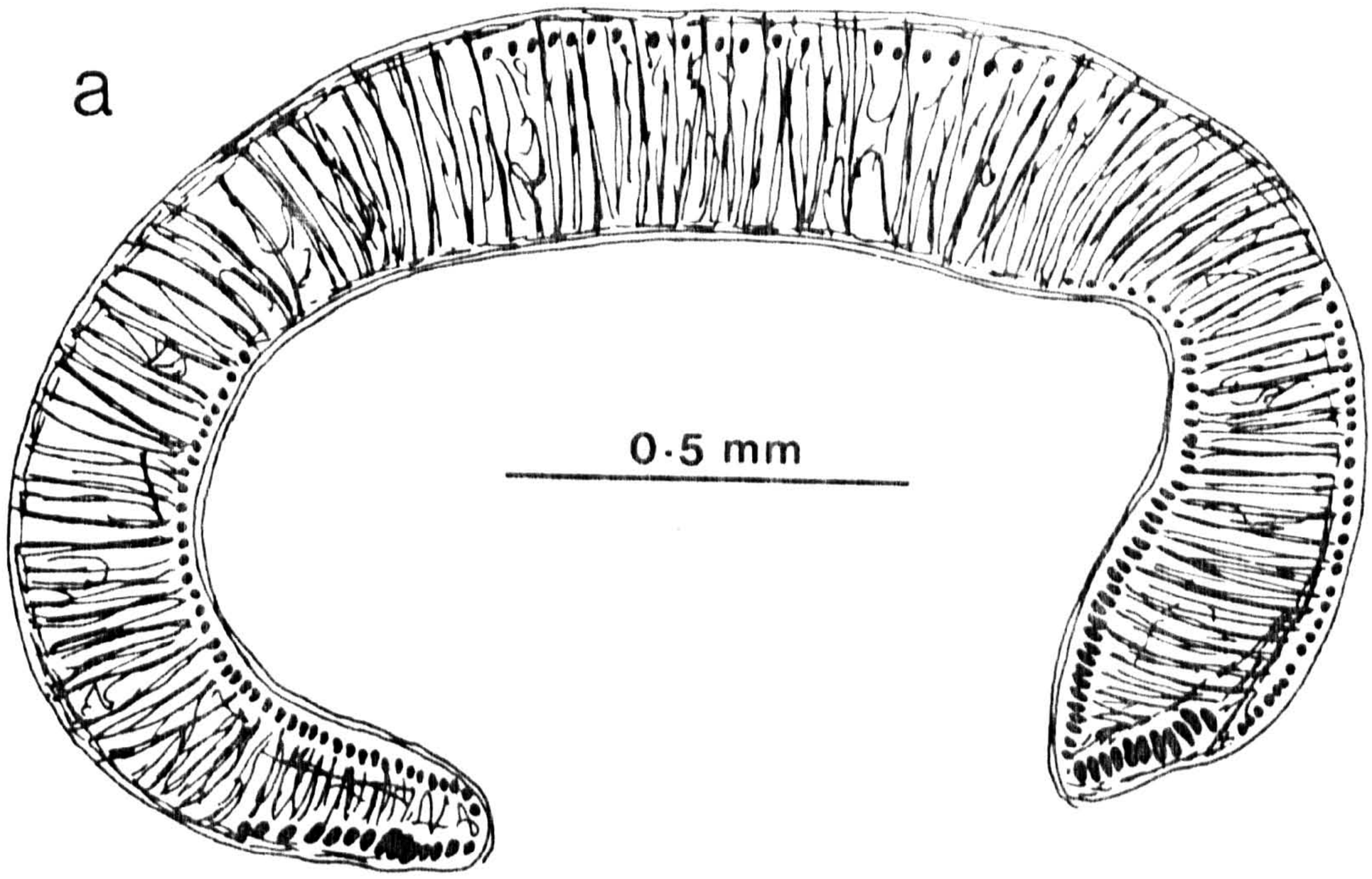
Types of acetabulum (iii)

(median sagittal section)

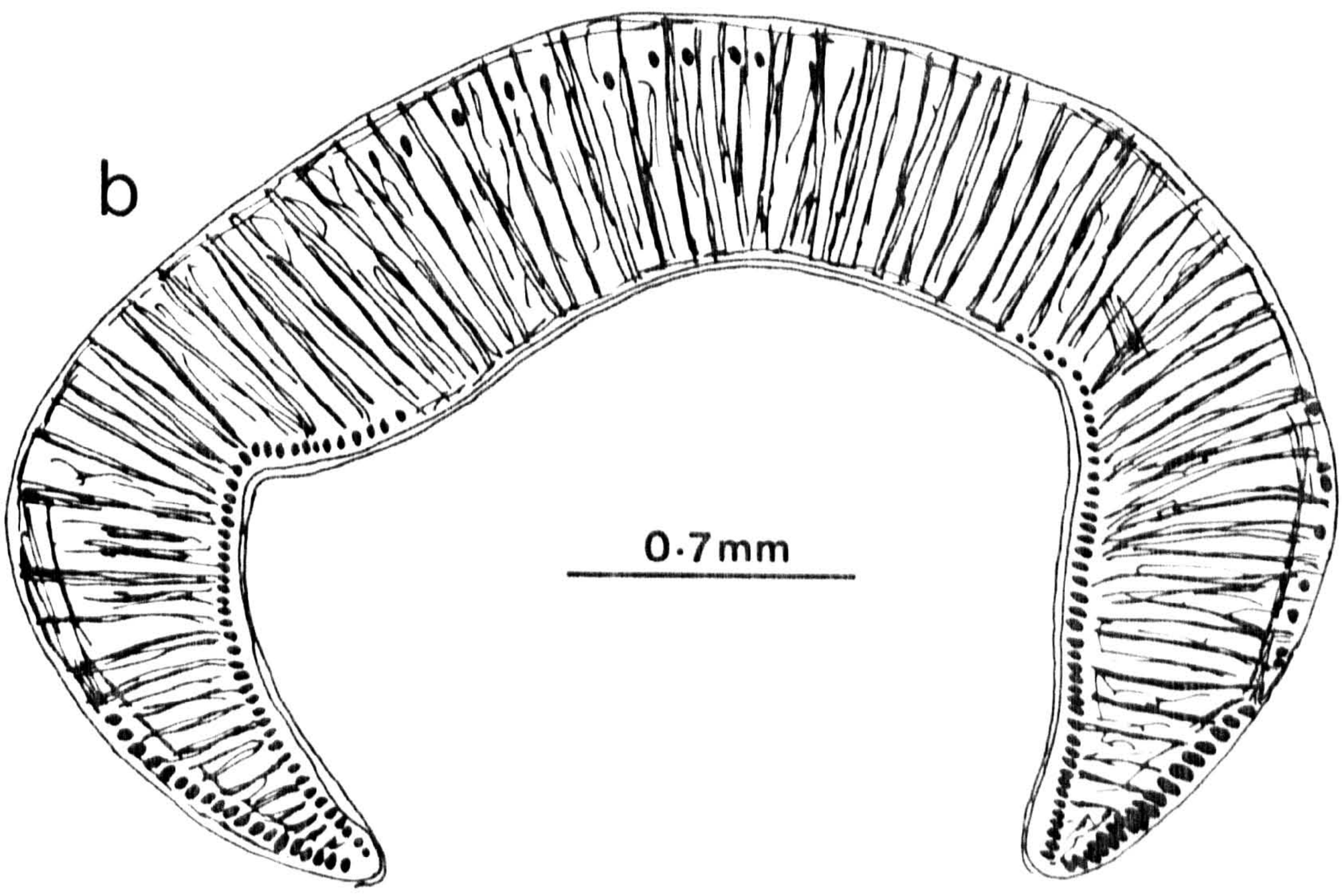
a. Paramphistomum type (Näsmark, 1937)

b. Pisum type (Näsmark, 1937), note the few and irregularly spaced units of the d.e.c.2 series.

a



b



fibres few and relatively weakly developed; exterior longitudinal fibres few but distinct.

6. Pisum type (Näsmark, 1937), Fig. 10b

Moderate in size. Resembles the paramphistomum type with respect to the circular units and longitudinal fibres but the d.e.c.2 units are fewer in number and usually irregularly spaced than the d.e.c.1 units.

7. Calicophoron type (Näsmark, 1937), Fig. 11a

Moderate in size. Similar to the paramphistomum and pisum types especially with respect to the circular muscle units but the d.e.c. series consists only of a single group of units. Radial fibres fairly developed; oblique fibres few and weakly developed; exterior longitudinal fibres few but distinct.

8. Cotylophoron type (Näsmark, 1937), Fig. 11b

Moderate in size. Resembles the calicophoron type with respect to the circular muscle units. However, it is characterized by the presence of strong and well developed bands of oblique muscle fibres which lie along the interior borders of the d.e.c. and v.e.c. series. Radial fibres well developed; exterior longitudinal fibres few but distinct.

9. Streptocoelium type (Näsmark, 1937), Fig. 12a

Small in size. The d.e.c. and v.e.c. series, each consists only of a single group of units. All units in the circular series are relatively slightly developed and are almost equal in size but somewhat smaller at the beginning and end of each series. The units of the d.e.c. and v.e.c. series are similar in size. As to the number of units, those in the interior series are greater and

FIGURE 11

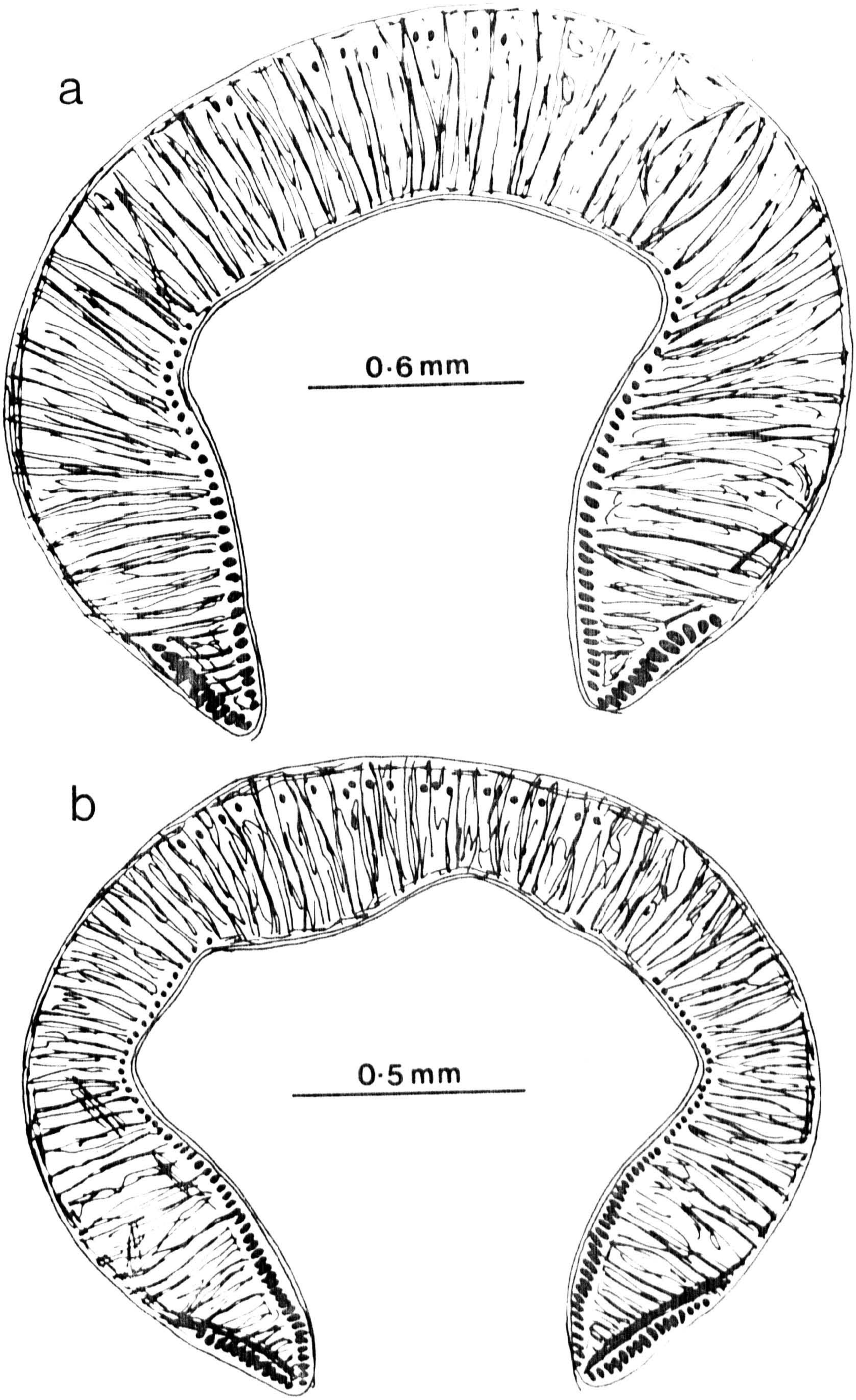
Types of acetabulum (iv)

(median sagittal section)

a. Calicophoron type (Näsmark, 1937)

b. Cotylophoron type (Näsmark, 1937)

a



0·6 mm

b

0·5 mm

slightly more developed than those in the exterior series. The m.e.c. series usually consists of irregularly spaced units. Radial fibres well developed and coarse; oblique fibres few and sometimes indistinct; exterior longitudinal fibres few but well developed.

10. Gastrothylax type (Näsmark, 1937), Fig. 12b

Moderate in size. It is characterized by a cavity of an almost flat bottom at right angle to the walls. Each of the circular series consists only of a single group of units and the units in all the series are well developed. As to the number of units, those in the exterior series consistently exceed those in the interior series. The m.e.c. series also consists of well developed units. Oblique fibres well developed; radial fibres strongly developed; exterior longitudinal fibres also well developed.

11. Stephanopharynx type (Näsmark, 1937), Fig. 12c

Moderate in size. The units in all the circular series are moderately developed and each series consists of a single continuous groups of units. The units in the interior series exceed in number those in the exterior series. Contrary to Nasmark's (1937) description, the units are smaller in size in the beginning of each series and gradually increase in size towards the end of the series. The units in the m.e.c. series are usually well developed. Radial fibres well developed, coarse and usually irregularly arranged; oblique fibres very few and indistinct; exterior longitudinal fibres well developed. The acetabular rim tapers to a point.

FIGURE 12

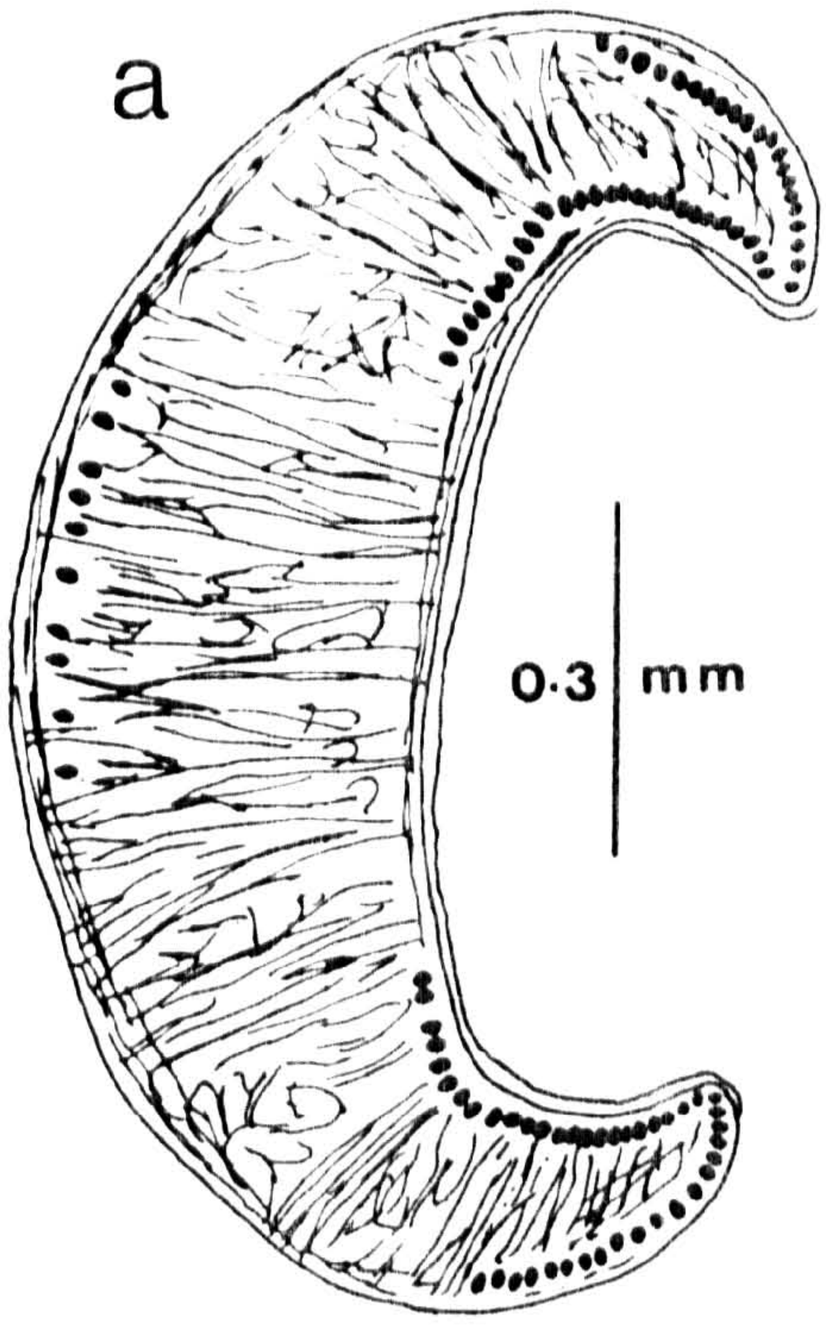
Types of acetabulum (v)

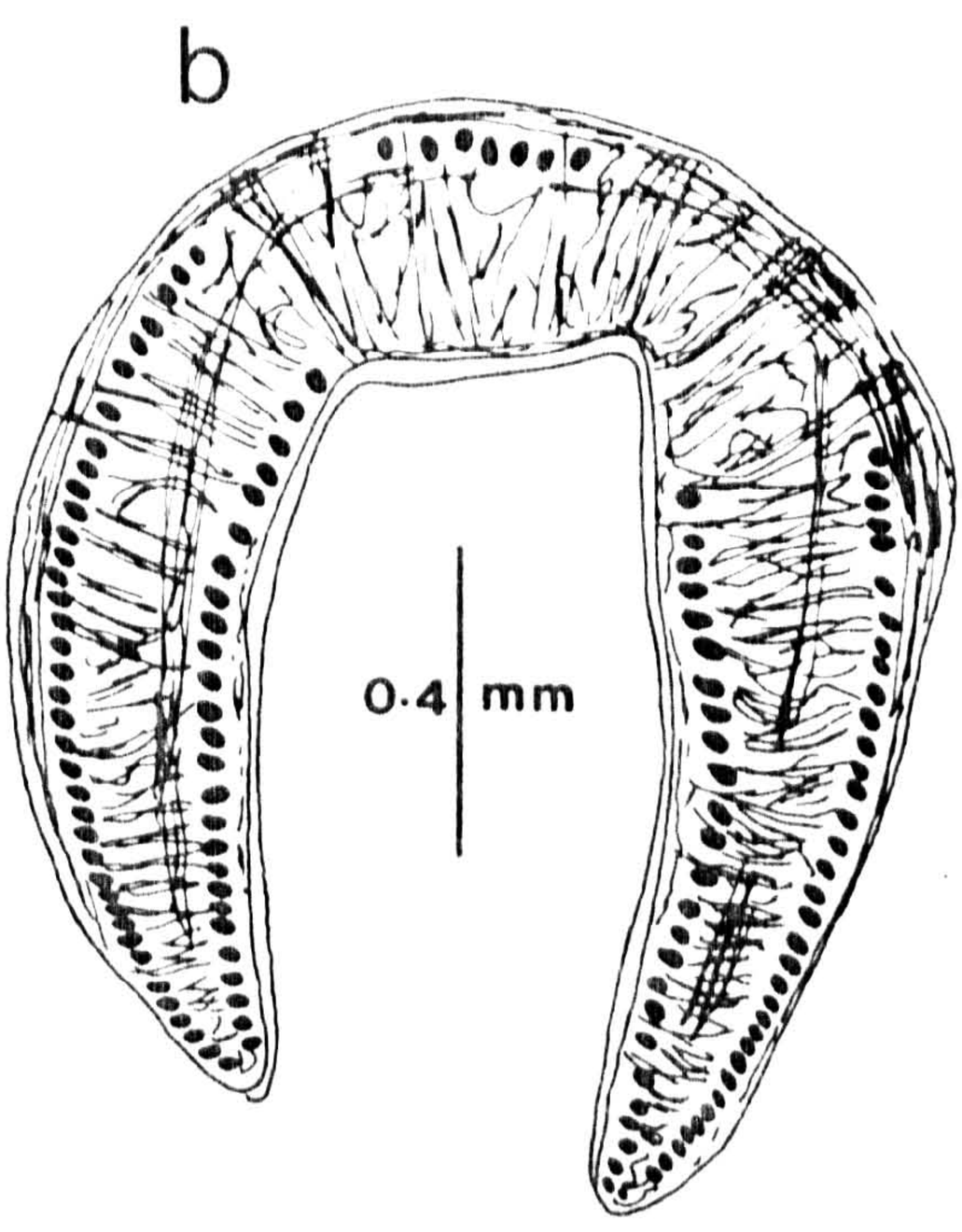
(median sagittal section)

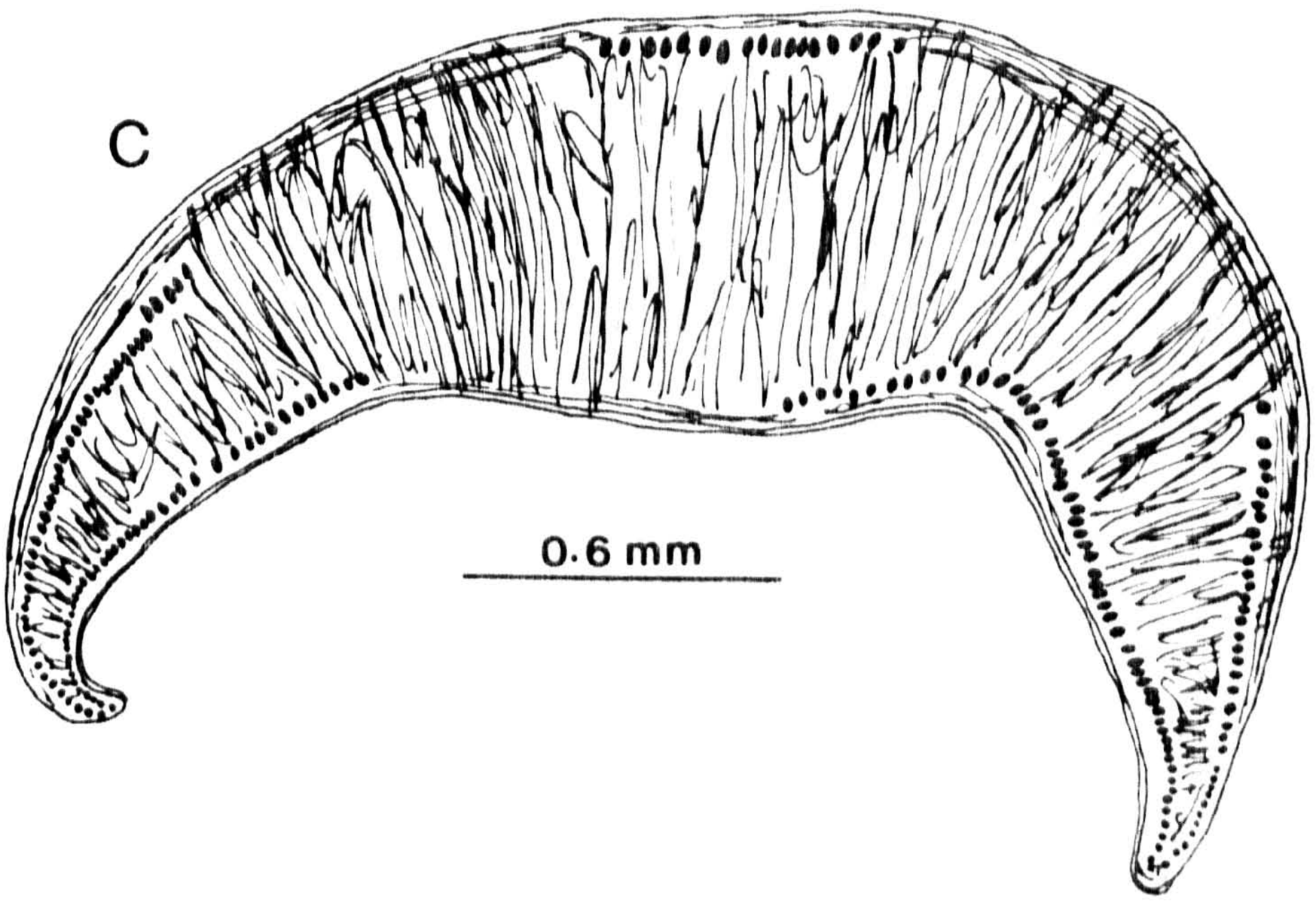
a. Streptocoelium type (Näsmark, 1937)

b. Gastrothylax type (Näsmark, 1937)

c. Stephanopharynx type (Näsmark, 1937)


a
0·3 mm


b
0·4 mm


C
0·6 mm

Key to the types of acetabulum observed among the different species examined in this work

1. Acetabulum enormous - 2

   Acetabulum not enormous - - - - - - - - - - - - - - - - - - - 4

2. Ventral exterior circular series divided into two groups, v.e.c.1 and v.e.c.2 - - - - - - - - - - - - - Gigantocotyle

   Ventral exterior circular series not divided into two groups - 3

3. Dorsal exterior circular 2 units smaller in size but greater in number than dorsal exterior circular 1 units; median exterior circular units present - - - - - - - - Explanatum

   Dorsal exterior 2 units smaller in size and number than the dorsal exterior circular 1 units; median exterior circular units present - - - - - - - - - - - - - - - Symmeri

   Dorsal exterior circular 2 units larger in size and greater in number than dorsal exterior circular 1 units; median exterior circular units absent - - - - - - Duplicitestorum

4. Dorsal exterior circular series divided into two groups of units, d.e.c.1 and d.e.c.2 - - - - - - - - - - - - - - - - 5

   Dorsal exterior circular series not divided into two groups of units - 6

5. Dorsal exterior circular 2 units smaller in size but greater in number than the dorsal exterior circular 1 units - - - - - - - - - - - - - - - - - - - Paramphistomum

   Dorsal exterior circular 2 units smaller in size, fewer in number and irregularly spaced than the dorsal exterior circular 1 units - Pisum

6. Exterior circular series (dorsal and ventral) consistently exceeds in number of units those in the interior circular series (dorsal and ventral) - - - - Gastrothylax

Exterior circular series lesser in number of units than those in the interior circular series - - - - - - - - - - 7

7. Band of oblique fibres bordering the inner margin of the exterior circular series well developed and prominent; exterior circular units compact and well developed but much lesser in number than the interior circular units - Cotylophoron

Band of oblique fibres bordering the inner margin of the exterior circular series weakly developed and not prominent; exterior circular units compact and well developed but much lesser in number than the interior circular units, sometimes the dorsal exterior circular units are formed into a sphincter - - - - - - Calicophoron

Band of oblique fibres bordering the inn margin of the exterior circular series absent; exterior circular units not compact and nearly equal in number those in the interior circular series - - - - - - - - - - - - - - - - - 8

8. Size small; radial fibres well developed and strong; size of units in each circular series is greater in the exterior and diminishes towards the interior of the series - Streptocoelium

Size medium; radial fibres not well developed; size of units in each circular series smallest in both exterior and interior ends of the series; acetabular rim tapers to a point - Stephanopharynx

THE PHARYNX

Like the acetabulum, the different types of pharynx established by Näsmark (1937) were based on the arrangement and development of the musculature as seen in median sagittal section. The types have proved very useful in the specific identification of members of the family.

Some types however were shown later to have been established based only on minor and inconsistent details. Dinnik (1964) has shown after a comparative study of the pharyngeal structure of several species from different hosts and localities that the paramphistomum, calicophoron and ijimai types of pharynx described by Näsmark (1937) are basically identical in structure and should be regarded as one and the same type. Since Paramphistomum cervi, the type species of the genus Paramphistomum possesses a liorchis type of pharynx, Dinnik (1964) proposed that the types in question should be called the calicophoron type. Sey (1974) seemed to have accepted Dinnik's view since he referred the pharynx of Paramphistomum daubneyi to the calicophoron type, following Dinnik, in his description of the species from specimens in Hungary. Sey and Graber (1979a) also referred to the same type in describing the pharynx of Cotylophoron macrosphinctris. From re-examination of Näsmark's original materials and examination of new materials, this study confirms the correctness of Dinnik's observation. The three above mentioned types are therefore referred here as the calicophoron type (sensu Dinnik, 1964).

Although Fischoeder (1903) in his original description of Paramphistomum orthocoelium has clearly indicated and illustrated the presence of an anterior sphincter in the pharynx of the species,

Näsmark (1937) has referred it to the paramphistomum type (=calicophoron type sensu Dinnik, 1964), a type which is characterized by the absence of an anterior sphincter. Careful re-examination however of Näsmark's material of the species by Eduardo (1980b) revealed the presence of the said structure but because of the poor staining, it appeared faint which may explain why Näsmark failed to observe it. Lee and Lowe (1971) have also observed the presence of an anterior sphincter in their material of the species in Malaya. Materials from China and the Philippines in this study all revealed the presence of an anterior sphincter.

The different types of pharynx, both new and already known ones, observed among the different species examined in this work are listed, defined and illustrated below. A schematic representation of a general type of pharynx adapted from Näsmark (1937) is also provided showing all features necessary for specific diagnosis (Fig. 13). Terminology is also that of Näsmark (1937).

Types of pharynx observed among the different species examined in this work

1. Dicranocoelium type (Näsmark, 1937), Fig. 14a-b

Characterized by the presence of a lip sphincter which is located in each lateral side of the anterior part of the pharynx and appears as a horse-shoe shape structure in sagittal section. Interior circular units fairly developed, middle circular units absent, basal circular units usually consist of a single row. Interior longitudinal fibres fairly developed, exterior longitudinal fibres few and very close to the exterior border, radial fibres moderately developed.

FIGURE 13

A schematic representation of a general type of pharynx as seen in median sagittal section showing details necessary for diagnosis (after Näsmark, 1937).

Key to abbreviations:

as - anterior sphincter
bc - basal circular units
ec - exterior circular units
el - exterior longitudinal fibres
ic - interior circular
il - interior longitudinal fibres
ls - lip sphincter
mc - middle circular units
ps - posterior sphincter
rf - radial fibres

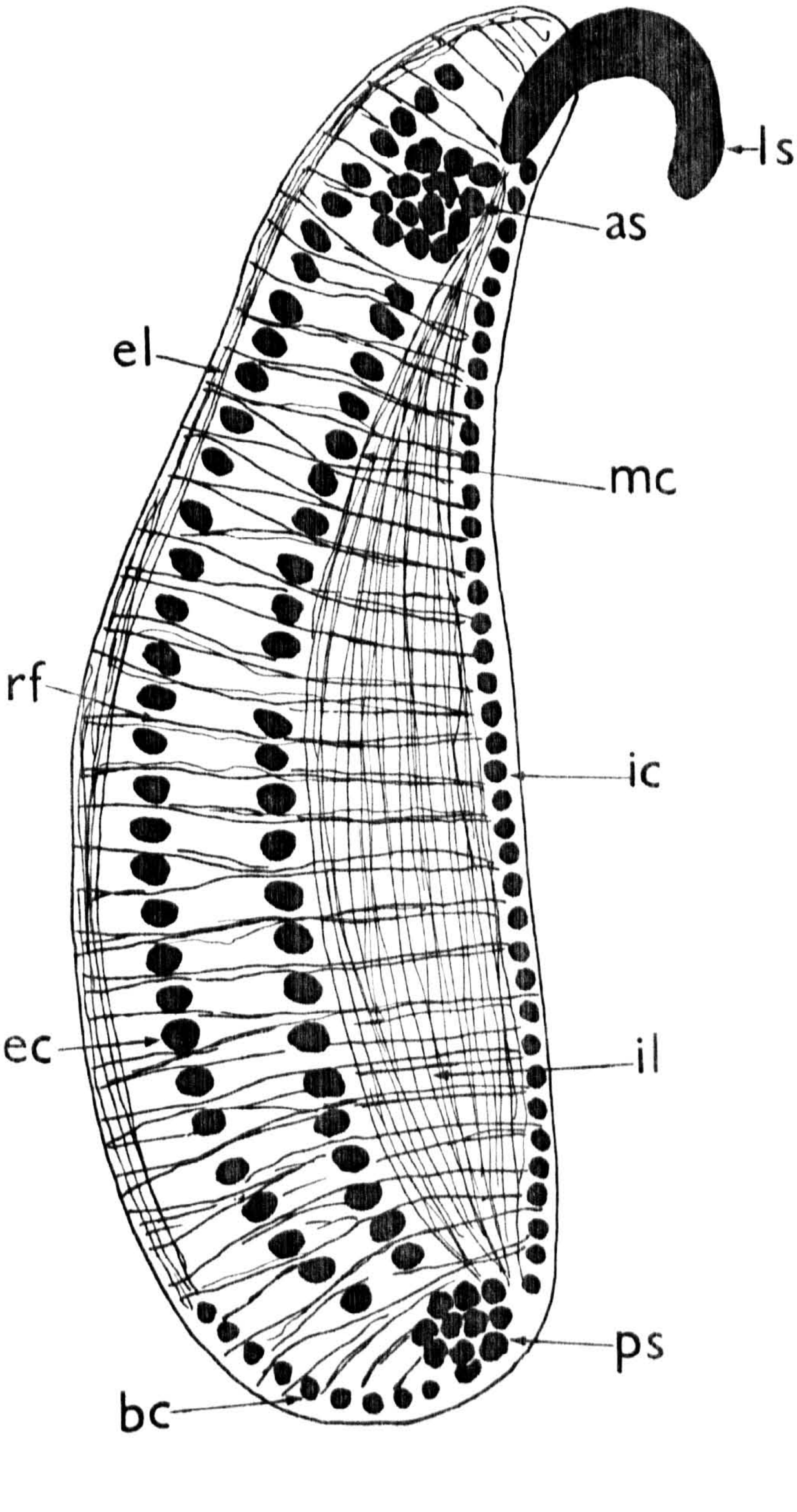

ls
as
el
mc
rf
ic
ec
il
ps
bc

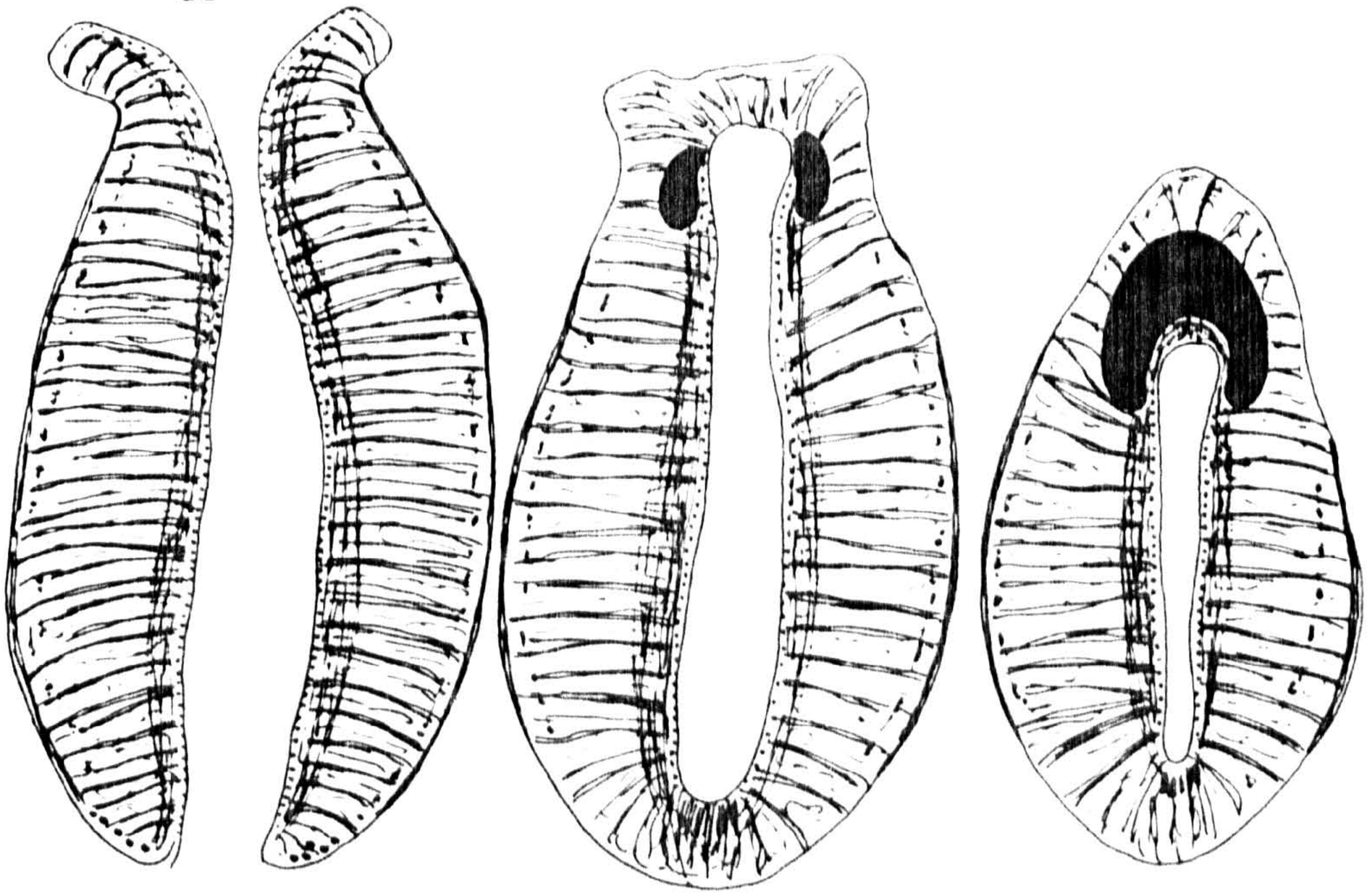
FIGURE 14

Types of pharynx (i)

a - b. Dicranocoelium type (Näsmark, 1937)

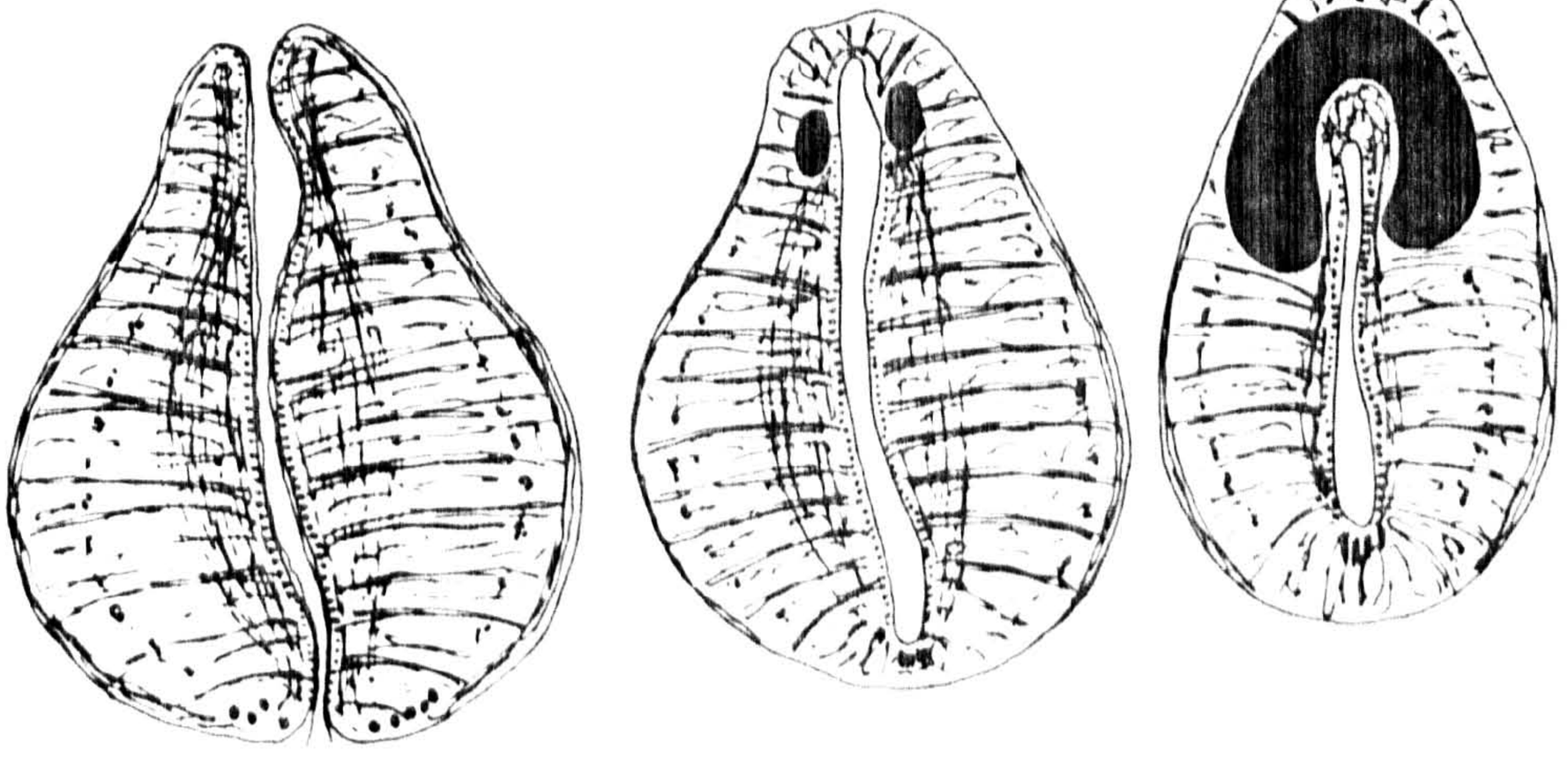
Sections at different sagittal planes, from median to lateral (left to right). Note that the lip sphincter can be seen only in lateral sagittal section.

a



b

0·2mm



2. Orthocoelium type (new type), Fig. 15a-b

Lip and posterior sphincters absent; anterior sphincter present and consists of closely packed circular units near the anterior end of the pharynx forming a nearly round to oval structure. Interior circular units fairly developed; middle and exterior circular units moderately developed, both series are joined together in their anterior and posterior limits; basal circular units moderately developed and consist of only a single series. Interior longitudinal fibres moderately developed and distinct; exterior longitudinal fibres few and close to the exterior border; radial fibres well developed.

3. Explanatum type (Näsmark, 1937), Fig. 15c-d

Lip sphincter absent; anterior and posterior sphincters present, the former strongly developed than the latter. Interior circular units moderately developed; middle circular units very strongly developed; exterior circular units moderately to very strongly developed but present only in the anterior part of the pharynx; basal circular units well developed, in single or double rows. Interior longitudinal fibres well developed and distinct; exterior longitudinal fibres few and close to the exterior border; radial fibres strongly developed.

FIGURE 15

Types of pharynx (ii)

(median sagittal section)

a - b. Orthocoelium type (new type)

c - d. Explanatum type (Näsmark, 1937)

e. Cephalophi type (new type)

a

b

0·4mm

c

d

e

0·3mm

0·3mm

0·1mm

4. Cephalophi type (new type), Fig. 15e

Lip and posterior sphincters absent; anterior sphincter present. Interior circular units weakly developed; middle circular units absent; exterior circular units present but confined only on the anterior part of the pharynx; basal circular units fairly developed. Interior longitudinal fibres moderately developed; exterior longitudinal fibres few and very close to the exterior border; radial fibres moderately developed.

5. Liorchis type (Näsmark, 1937)(=pseudoliorchis type of Velichko, 1966), Fig. 16a-d

Lip, anterior and posterior sphincters absent. Interior circular units weakly developed and sometimes indistinct; middle circular units well developed, each unit appears narrow and elongate transversely; exterior circular units well developed and closer to the middle circular series than to the exterior wall, both middle and exterior circular series terminate short of the anterior end of the pharynx; basal circular units moderately developed. Interior longitudinal fibres well developed and distinct; exterior longitudinal fibres few and close to the exterior wall; radial fibres well developed. Long papillae are present attached to the internal wall of the anterior part of the pharynx.

6. Calicophoron type (Dinnik, 1964)(=paramphistomum, calicophoron and ijimai types of Näsmark, 1937), Figs. 16e-f & 17a-c

Lip, anterior and posterior sphincters absent. Interior circular units moderately developed; middle circular units usually absent but may be present as poorly developed and indistinct series;

FIGURE 16

Types of pharynx (iii)

(median sagittal section)

a - d. Liorchis type (Näsmark, 1937)

e - f. Calicophoron type (Dinnik, 1954)(=paramphistomum, calicophoron and ijimai types of Näsmark, 1937)

a

b

c

0·2mm

d

e

f

0·2mm

0·2mm

0·2mm

exterior circular units fairly developed; basal circular units moderately developed. Interior longitudinal fibres moderately developed; exterior longitudinal fibres few and close to the exterior wall; radial fibres moderately developed.

7. Gigantopharynx type (new type), Fig. 17e

Lip, anterior and posterior sphincters absent. Interior circular units very poorly developed and present only in the anterior third of the pharynx; middle circular units absent; exterior circular units fairly developed and present only in the posterior 2/3 of the pharynx close to the exterior longitudinal fibres; basal circular units moderately developed. Longitudinal fibres absent but there are few and weakly developed fibres in the anterior third near the interior circular units. In the base of the pharynx is a small area of fine fibres running from anterior to posterior direction. Exterior longitudinal fibres few but distinct and close to the exterior wall; radial fibres fairly developed. Long papillae are present attached to the interior wall of the anterior third of the pharynx.

8. Stephanopharynx type (Näsmark, 1937), Fig. 18a-b

This type is easily distinguished by the presence of an unpaired diverticulum. Lip, anterior and posterior sphincters absent. Interior circular units fairly developed; middle, exterior and basal circular units absent. Few well developed strands of longitudinal fibres present but not arranged into distinct interior and exterior layers, rather randomly arranged; radial fibres well developed and coarse. Musculature of wall of diverticulum consists of loose network of fibres, internal surface has long papillae which

FIGURE 17

Types of pharynx (iv)

(median sagittal section)

a - d. Calicophoron type (Dinnik, 1964)(=paramphistomum, calicophoron and ijimai types of Näsmark, 1937)

e. Gigantopharynx type (new type)

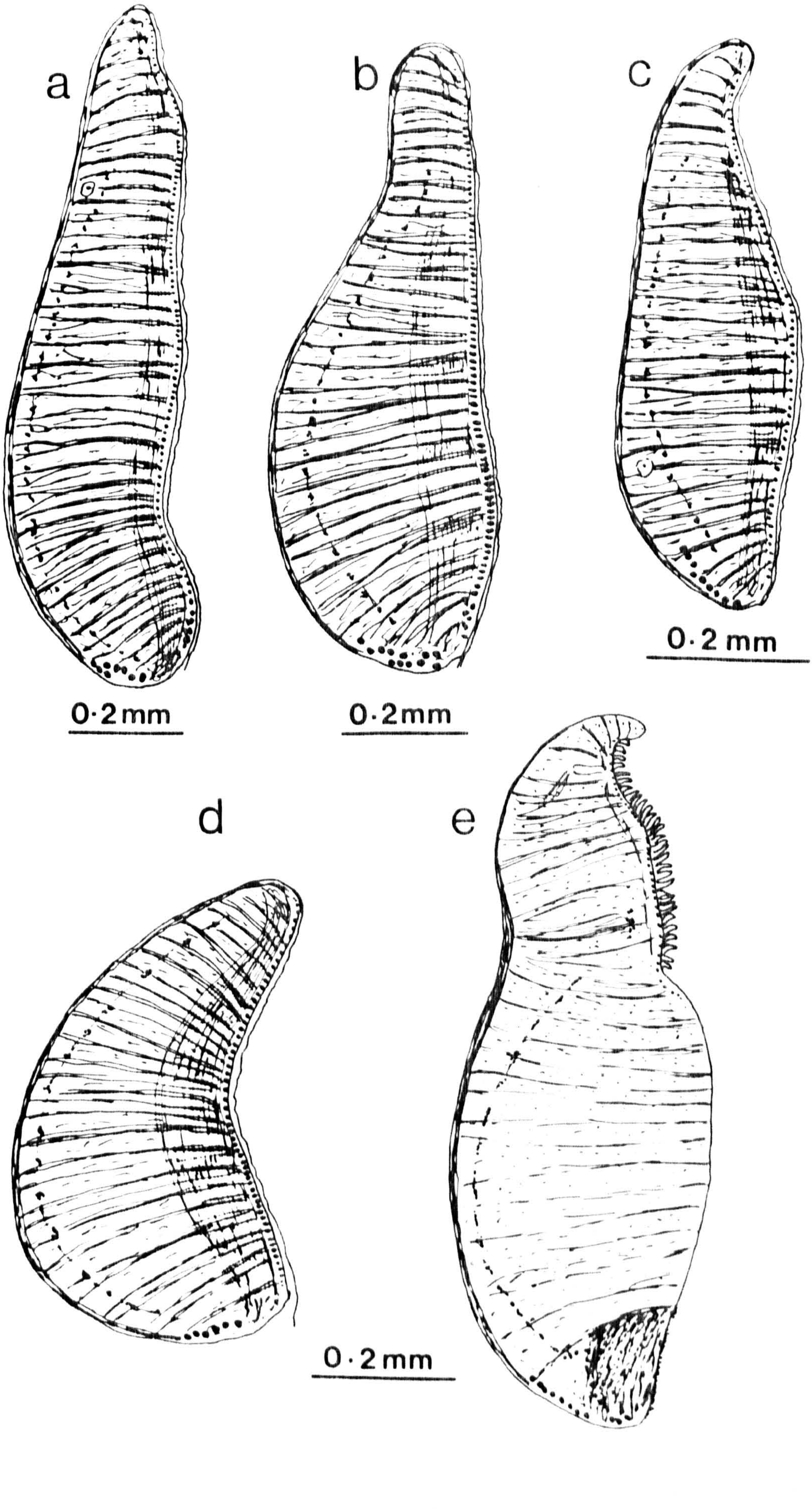

a
0·2mm
b
0·2mm
c
0·2 mm
d
0·2mm
e
0·2mm

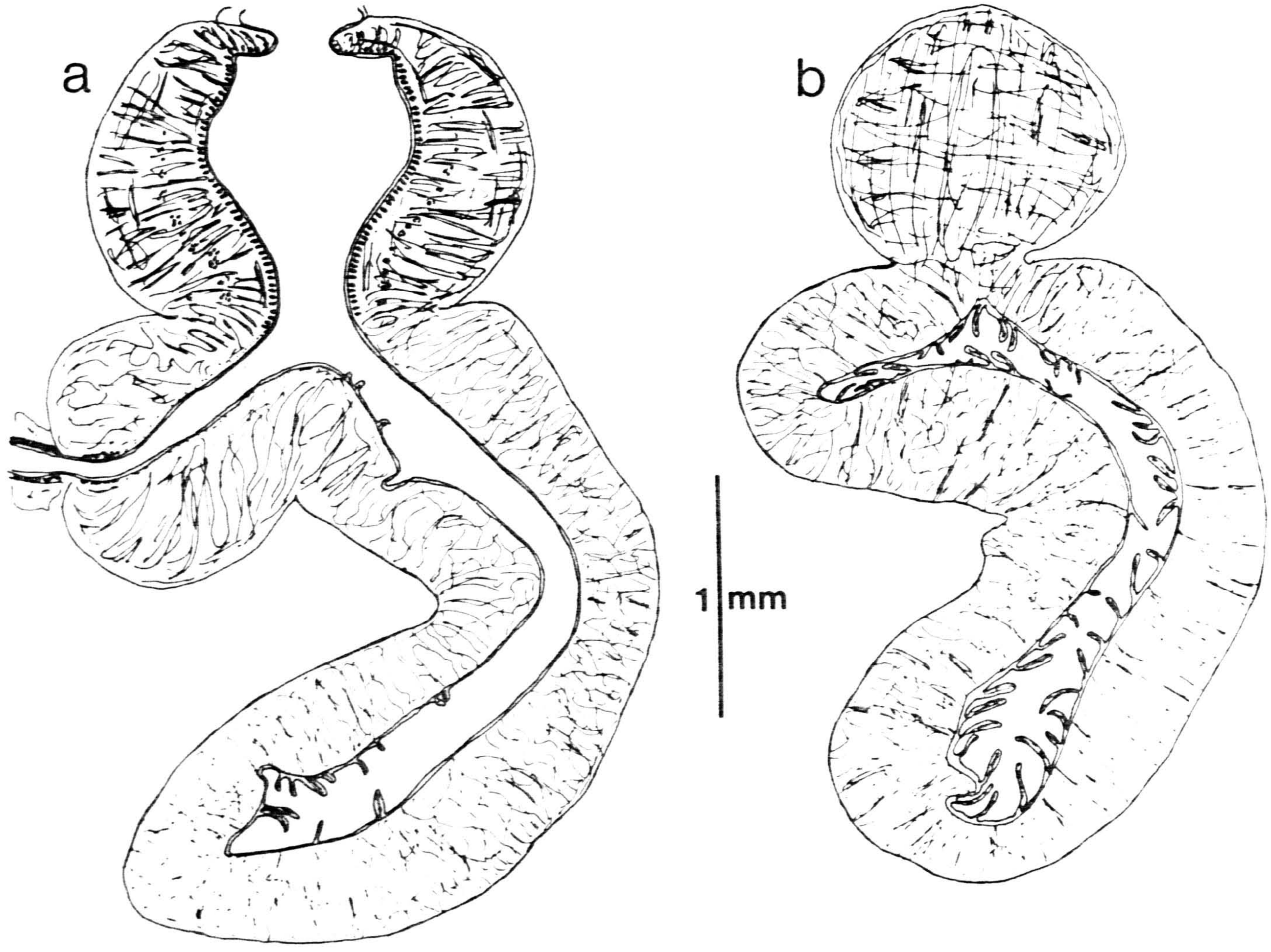
FIGURE 18

Types of pharynx (v)

Stephanopharynx type (Näsmark, 1937)

a. Median sagittal section

b. Lateral sagittal section, note concentration of papillae in this section.


a
b
1 mm

are present and concentratd only on the lateral corners of the diverticulum.

9. Balanorchis type (new type), Fig. 19a-b

This type resembles the stephanopharynx type with respect to the mausculature but differs from it by its smaller size and the presence of a smaller but paired diverticula. Papillae are absent on the internal surface of the diverticula.

FIGURE 19

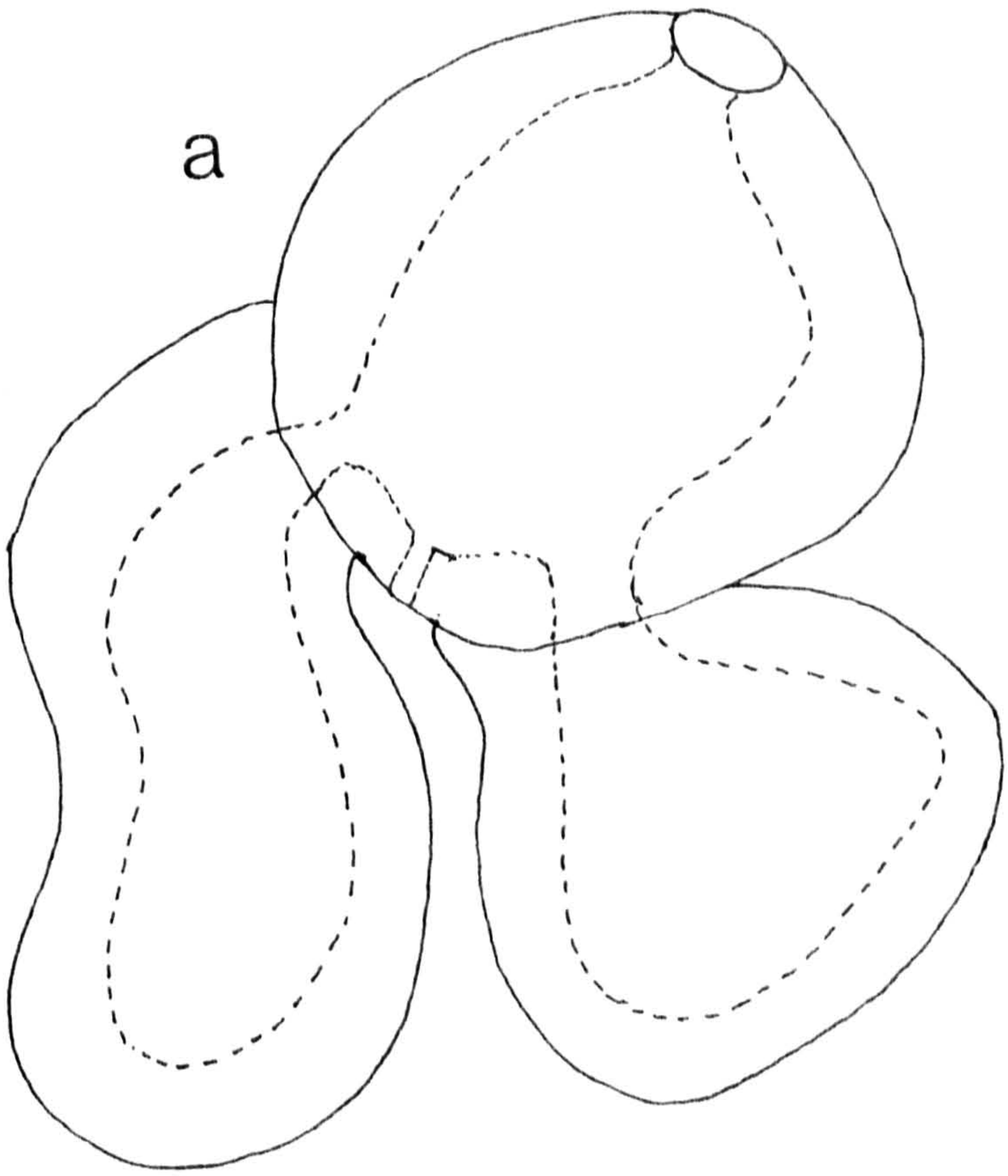
Types of pharynx (vi)

Balanorchis type (new type)

a. Ventral view, note paired diverticula.

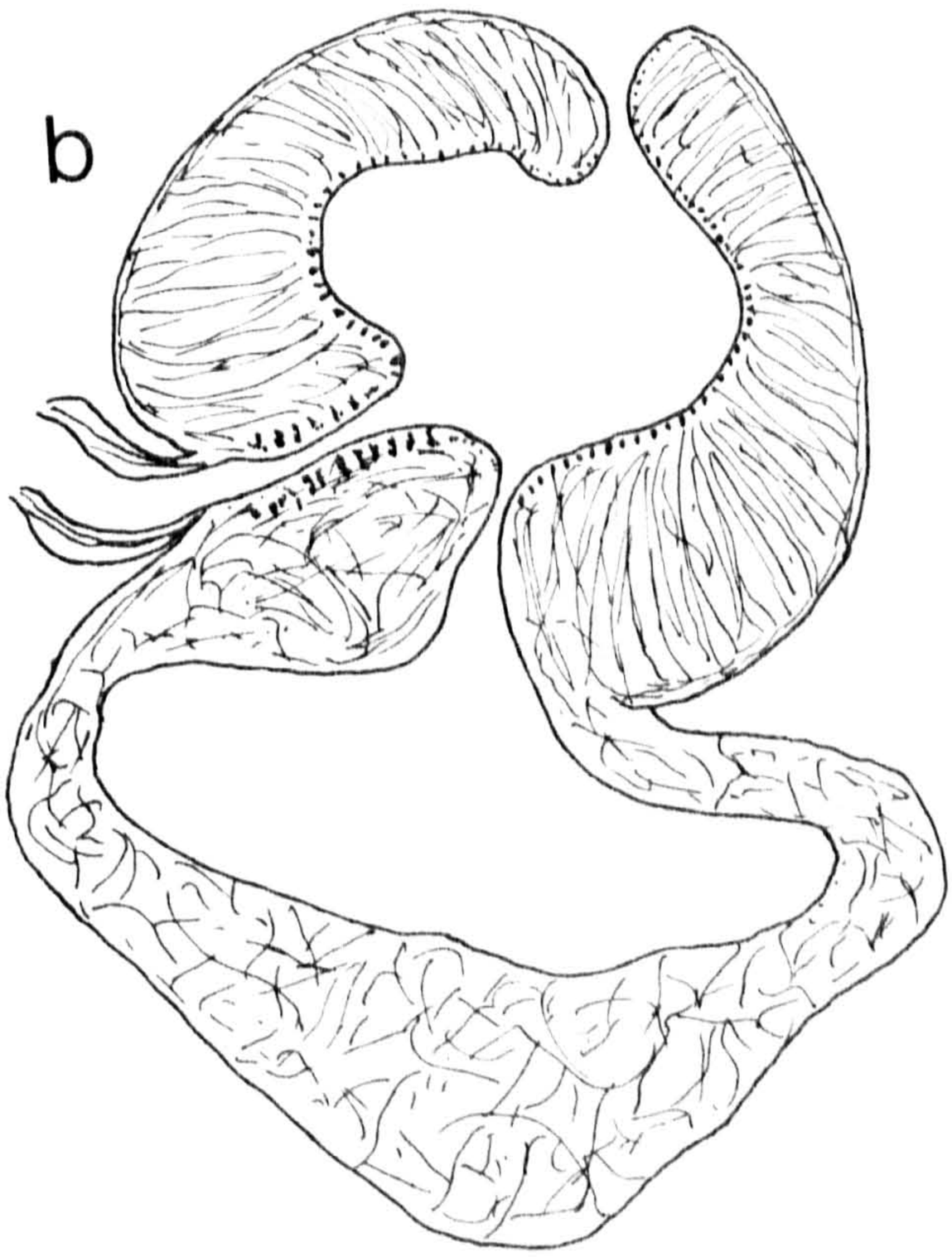
b. Median sagittal section

a



0.1 mm

b



Key to the types of pharynx observed among the different species examined in this work

1. Pharyngeal diverticulum present - - - - - - - - - - - - - - - - 2

   Pharyngeal diverticulum absent - - - - - - - - - - - - - - - - - 3

2. Diverticulum unpaired and enormous; interior circular units of pharynx proper well developed - - - - - Stephanopharynx

   Diverticulum paired; interior circular units of pharynx proper weakly developed - - - - - - - - - - - - Balanorchis

3. Lip sphincter present - - - - - - - - - - - - - - - Dicranocoelium

   Lip sphincter absent - 4

4. Anterior sphincter present - - - - - - - - - - - - - - - - - - 5

   Anterior sphincter absent - - - - - - - - - - - - - - - - - - - 7

5. Posterior sphincter present - - - - - - - - - - - - - - Explanatum

   Posterior sphincter absent - - - - - - - - - - - - - - - - - - - 6

6. Exterior and middle circular series fairly developed, occupy the greater length of the pharynx and join together in their anterior and posterior limits - - - Orthocoelium

   Exterior circular series well developed but present only in the anterior part of the pharynx; middle circular series absent - - - - - - - - - - - - - - - - - - Cephalophi

7. Exterior and middle circular series well developed; internal surface with long papillae - - - - - - - - - - - - Liorchis

   Exterior circular series weakly to moderately developed; middle circular series usually absent, if present weakly developed; internal surface without long papillae - Calicophoron

   Exterior circular series weakly developed; middle circular and longitudinal fibres absent; internal surface with long papillae on the anterior part - - - - Gigantopharynx

THE TERMINAL GENITALIUM

Näsmark (1937) used the term genital atrium to indicate the whole terminal structure of the genital system that opens into the outside through the genital pore. This includes the genital papilla and the folds of wall surrounding it and the different cavities therein enclosed. At the same time and without giving any reason, he employed the same term to refer to the cavity surrounding the genital papilla and enclosed by the genital fold. To avoid confusion, it is here proposed that the term genital atrium should refer only to the cavity surrounding the genital papilla and enclosed by the genital fold to differentiate it from another cavity which may be present and ventral to it called the ventral atrium and the whole terminal structure should be called the terminal genitalium.

Näsmark (1937) in his schematic representation of a general type of terminal genitalium as seen in median sagittal section has introduced terms and labeled all the parts except for two structures which are unlabeled. These are the two folds each enclosing a cavity, the genital atrium and the ventral atrium. Dinnik (1962) gave the term genital fold for that enclosing the genital atrium. However, no name was given for the second fold which is ventral and external to the genital fold and enclosing the ventral atrium. The fold in question is lacking in the majority of paramphistomid species but present in Paramphistomum bothriophoron and P. papilligerum. Following the terminology used for the cavity enclosed by this fold, the term ventral fold is here proposed for it.

Based on the development of the musculature of the terminal genitalium, Näsmark (1937) established different types observed

among the different species available to him at that time. The types observed among the different species examined in this work are listed, defined and illustrated below. These include both new and already known types of terminal genitalium. To show the features necessary for diagnosis and the terms employed here, a schematic representation of a general type of terminal genitalium adapted but modified from Näsmark (1937) is also provided.

Types of terminal genitalium observed among the different species examined in this work

1. Bothriophoron type (Näsmark, 1937), Fig. 21a-c

True ventral fold and ventral atrium present; ventral sphincter well developed. Genital fold, genital papilla and genital atrium small and lie at the bottom of the large ventral atrium; genital sphincter and sphincter papilla weakly developed but distinct. Radial fibres moderately developed.

2. Clavula type (Näsmark, 1937), Fig. 22a-b

Genital fold well developed and forms the wall of the whole terminal structure; genital sphincter compact, enormous and strong; genital papilla usually thick, clumsy and retracted; sphincter papilla moderately developed. Radial fibres well developed.

True ventral fold and ventral atrium absent. However, they may be formed artificially when the genital fold and papillae are retracted but are lost when these are in the normal state of relaxation.

FIGURE 20

A schematic representation of a general type of terminal genitalium as seen in median sagittal section showing features necessary for diagnosis (modified from Näsmark, 1937).

Key to abbreviations:

ga - genital atrium
gf - genital fold
gp - genital pore
gpl - genital papilla
gs - genital sphincter
rf - radial fibres
spl - sphincter papilla
va - ventral atrium
vf - ventral fold
vs - ventral sphincter

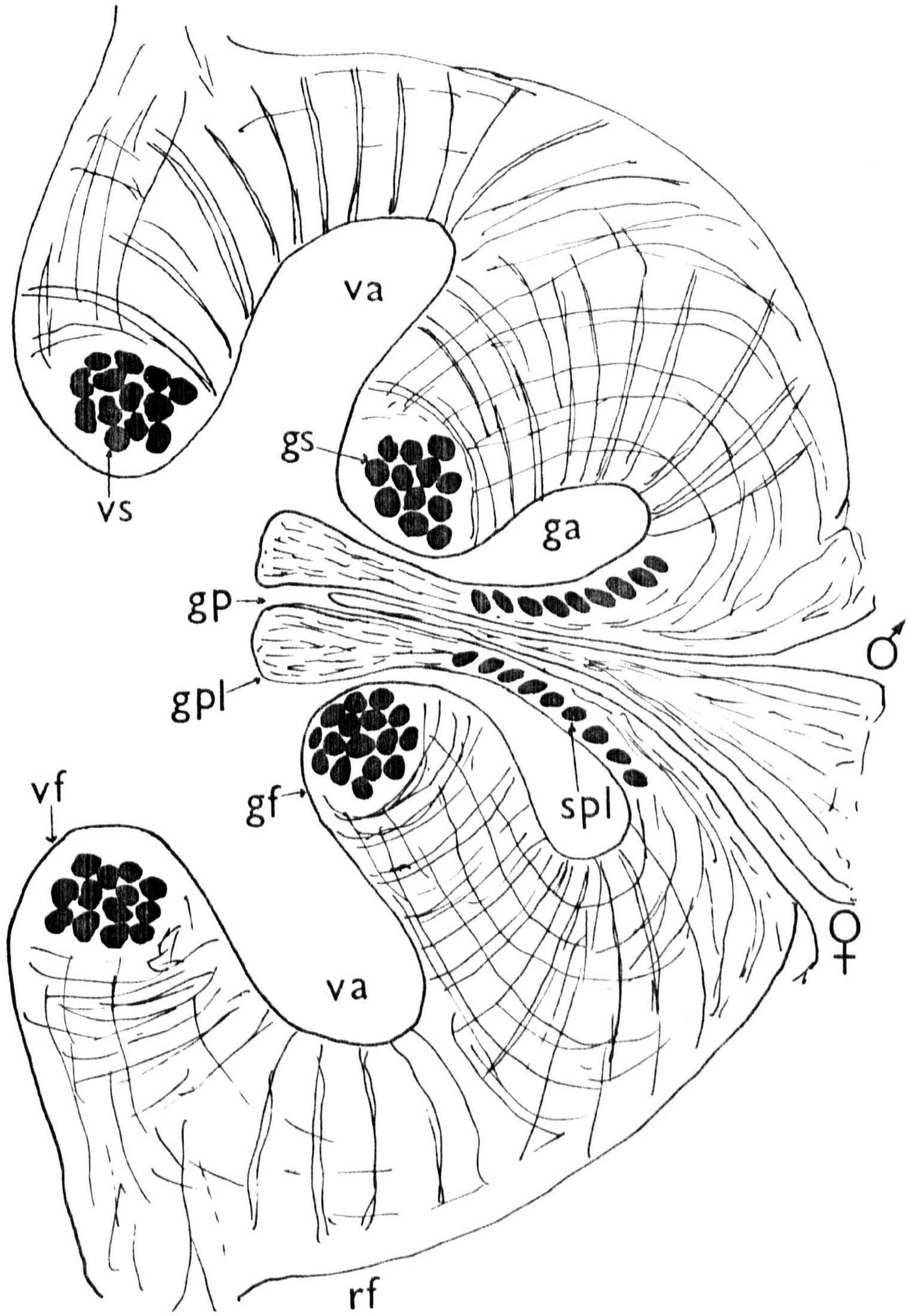
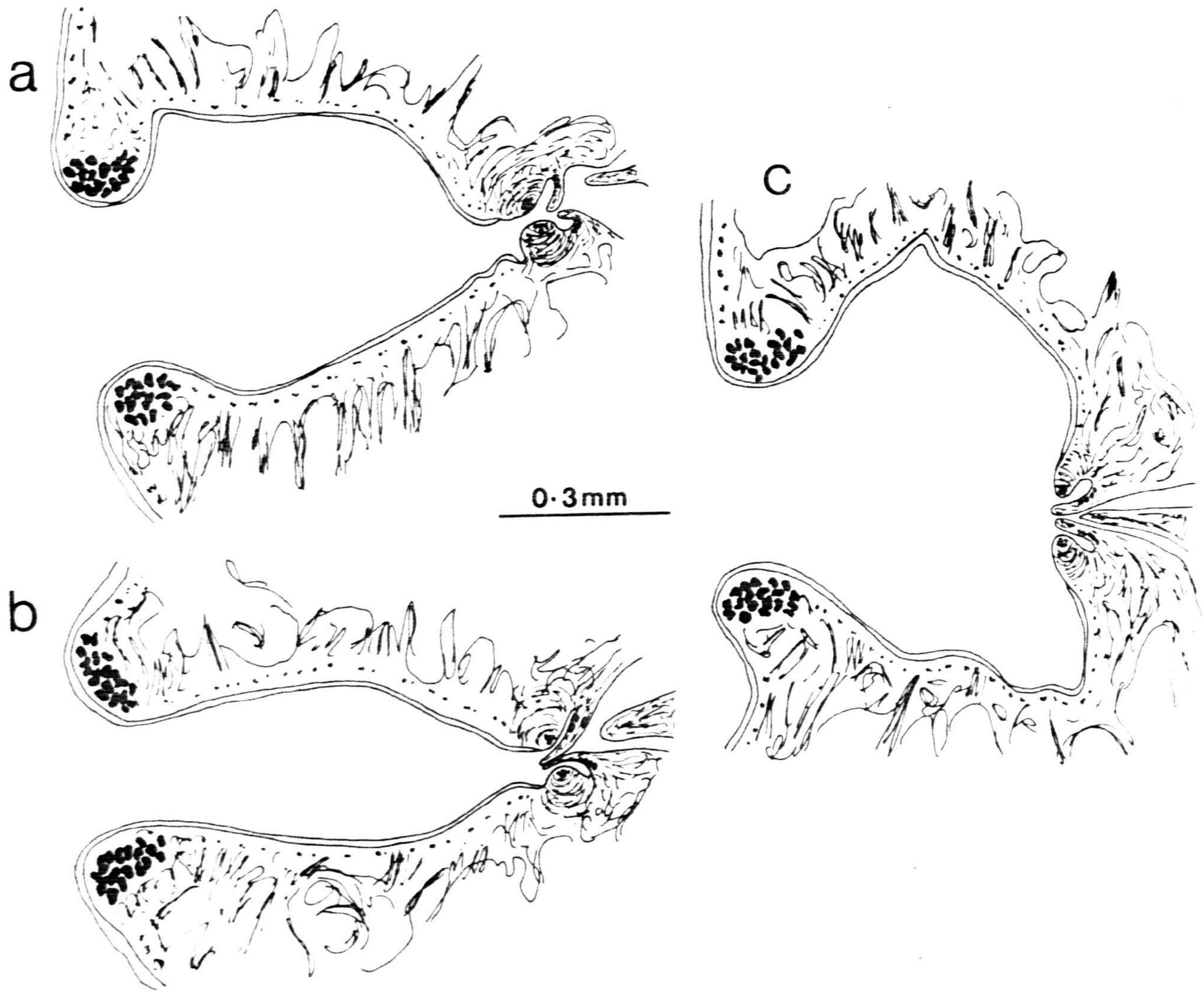

va
vs
gs
ga
gp
gpl
♂
spl
gf
vf
va
♀
rf

FIGURE 21

Types of terminal genitalium (i)

(median sagittal section)

a - c. Bothriophoron type (Näsmark, 1937) at various degrees of relaxation. Note the presence of a roomy ventral atrium and well developed ventral fold in all forms.


a
b
c
0·3mm

3. Streptocoelium type (Näsmark, 1937), Fig. 22c

Genital fold fairly developed; genital sphincter well developed and strong; genital papilla well developed; sphincter papilla strong and continuous joining the genital sphincter. Radial fibres fairly developed. True ventral fold and ventral atrium absent.

4. Orthocoelium type (new type), Fig. 22d

Genital fold well developed and strongly curved inwards; genital sphincter well developed; genital papilla thick and broad; sphincter papilla well developed. Radial fibres strongly developed. True ventral fold and ventral atrium absent.

Näsmark (1937) has referred the terminal genitalium of Orthocoelium orthocoelium to the gracile type, i.e. absence of genital sphincter and sphincter papilla. Re-examination of Näsmark's original sections of the species however revealed the presence of the above structures but they appeared faint because of the poor staining which may explain why Näsmark failed to observe them. New materials of the species from the Philippines and China examined in this work and materials from Malaysia examined by Lee and Lowe (1971) revealed the presence of these structures. The latter author however referred the pharynx of their specimens to the streptocoelium type.

5. Gigantocoyle type (Näsmark, 1937), Fig. 23a-d

Whole structure is characteristically large. Genital papilla enormous; genital sphincter and sphincter papilla appear less developed in relation to the large size of the whole terminal structure. Radial fibres well developed. Ventral fold and ventral atrium absent.

FIGURE 22

Types of terminal genitalium (ii)

(median sagittal section)

a - b. Clavula type (Näsmark, 1937). Note that artificial shallow ventral atrium and ventral fold are formed as a result of the retraction of the genital fold and genital papilla (a) but are absent when these are normally relaxed (b).

c. Streptocoelium type (Näsmark, 1937)

d. Orthocoelium type (new type)

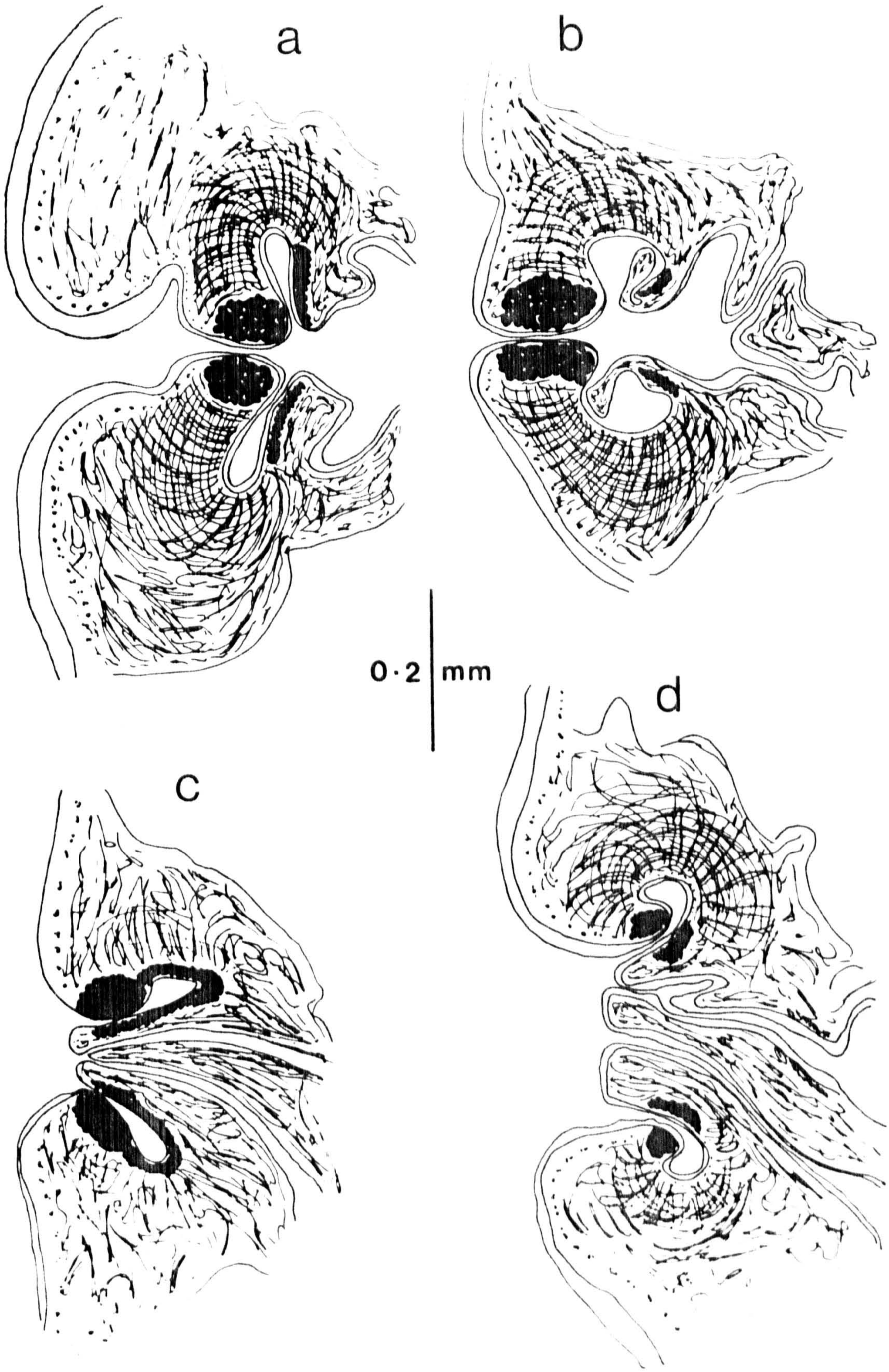
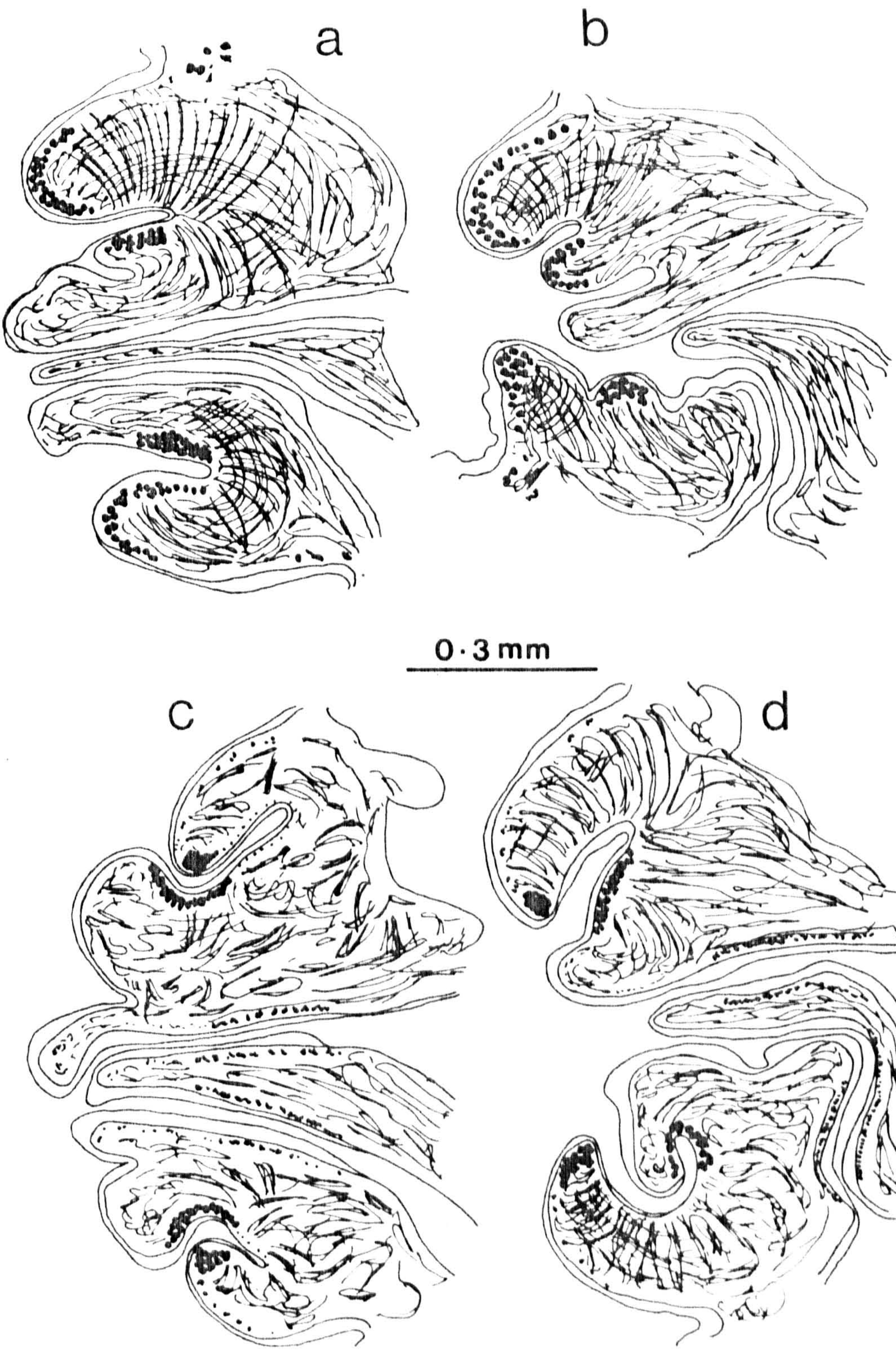

a
b
0·2 mm
c
d

FIGURE 23

Types of terminal genitalium (iii)

(median sagittal section)

a - d. Gigantocotyle type (Näsmark, 1937) at various degrees of relaxation.


a
b
0·3 mm
c
d

6. Calicophoron type (Näsmark, 1937) Figs. 4a-c, 24a-c

Characterized by the presence of a retractable genital pillar or column. Genital fold and genital papilla small and surmounted on the free end of the genital pillar. Genital sphincter and sphincter papilla slightly developed but distinct. Radial fibres well developed. True ventral fold and ventral atrium absent.

7. Raja type (new type), Figs. 4d-f, 25a-c

Similar to the calicophoron type in all respect except for the presence of minute tegumental papillae lining the surface of the genital pillar or column.

8. Microbothrium type (Näsmark, 1937), Fig. 26a-d

Genital fold well defined; genital sphincter fairly developed and distinct; genital papilla fairly developed and slender; sphincter papilla weakly developed but distinct. Radial fibres well developed. True ventral fold and ventral atrium absent but may be formed artificially when the genital papilla and genital fold are strongly retracted but these are lost when the latter are normally relaxed.

9. Scoliocoelium type (Näsmark, 1937) Fig. 27a-b

This type resembles the microbothrium type but the whole structure is smaller and the genital sphincter is well developed approaching that of the clavula type. Radial fibres well developed. True ventral fold and ventral atrium absent.

10. Papillogenitalis type (Eduardo, 1980a), Fig. 27c-e

Resembles the microbothrium type but the whole structure is smaller and external surface of the genital fold is lined by tegumental papillae. Radial fibres well developed. Artificial

FIGURE 24

Types of terminal genitalium (iv)

(median sagittal section)

a - c. Calicophoron type (Näsmark, 1937). Note presence of a genital pillar or column, everted as in a and retracted as in b & c. See also figure 4a-c.

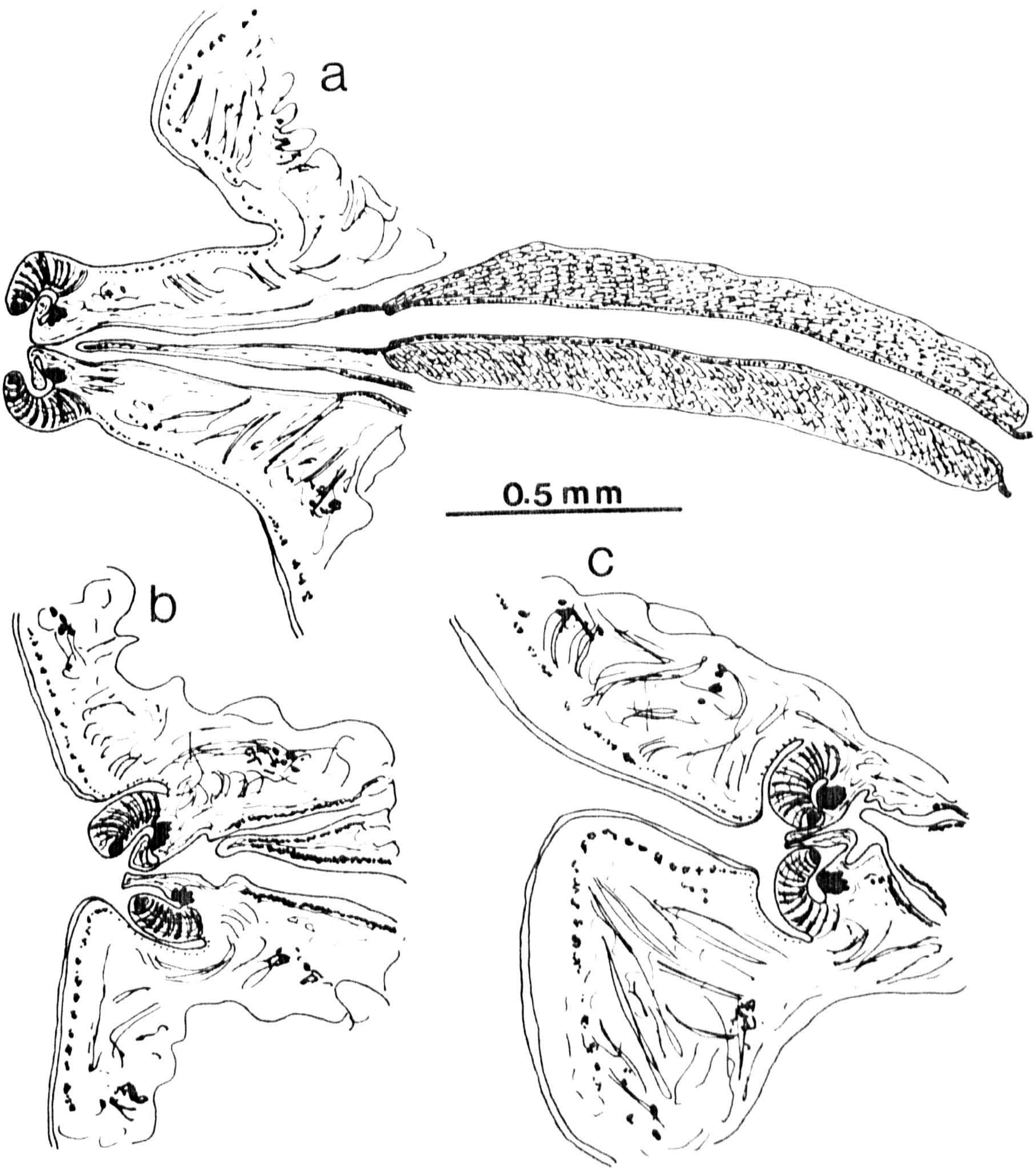

a
b
c
0.5 mm

FIGURE 25

Types of terminal genitalium (v)

(median sagittal section)

a - c. Raja type (new type). Note presence of a genital pillar or column, fully everted (a), partly everted (b) and retracted (c) and also the presence of minute papillae on the surface of the pillar. See also figure 4d-f.

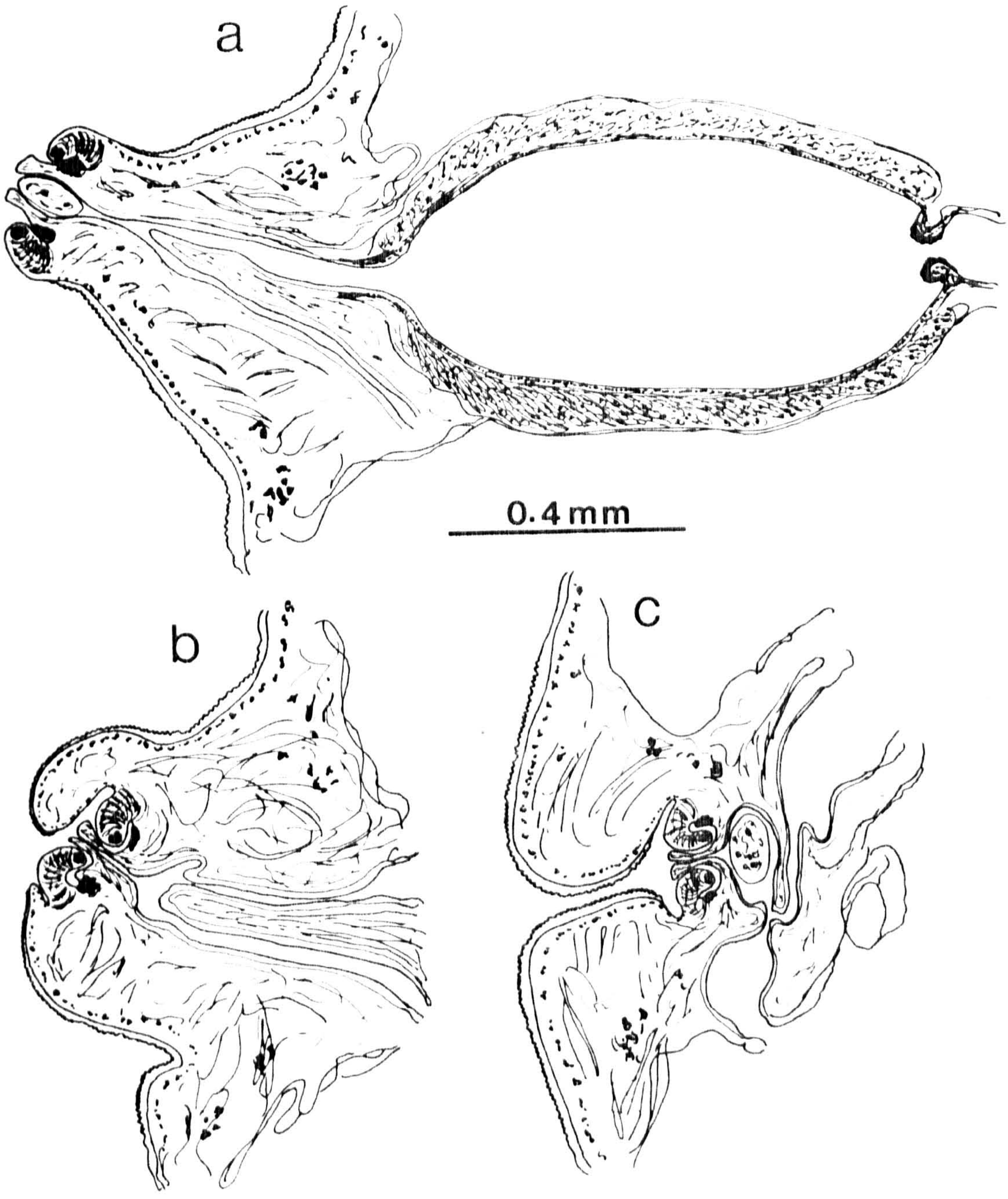

a
0.4 mm
b
c

FIGURE 26

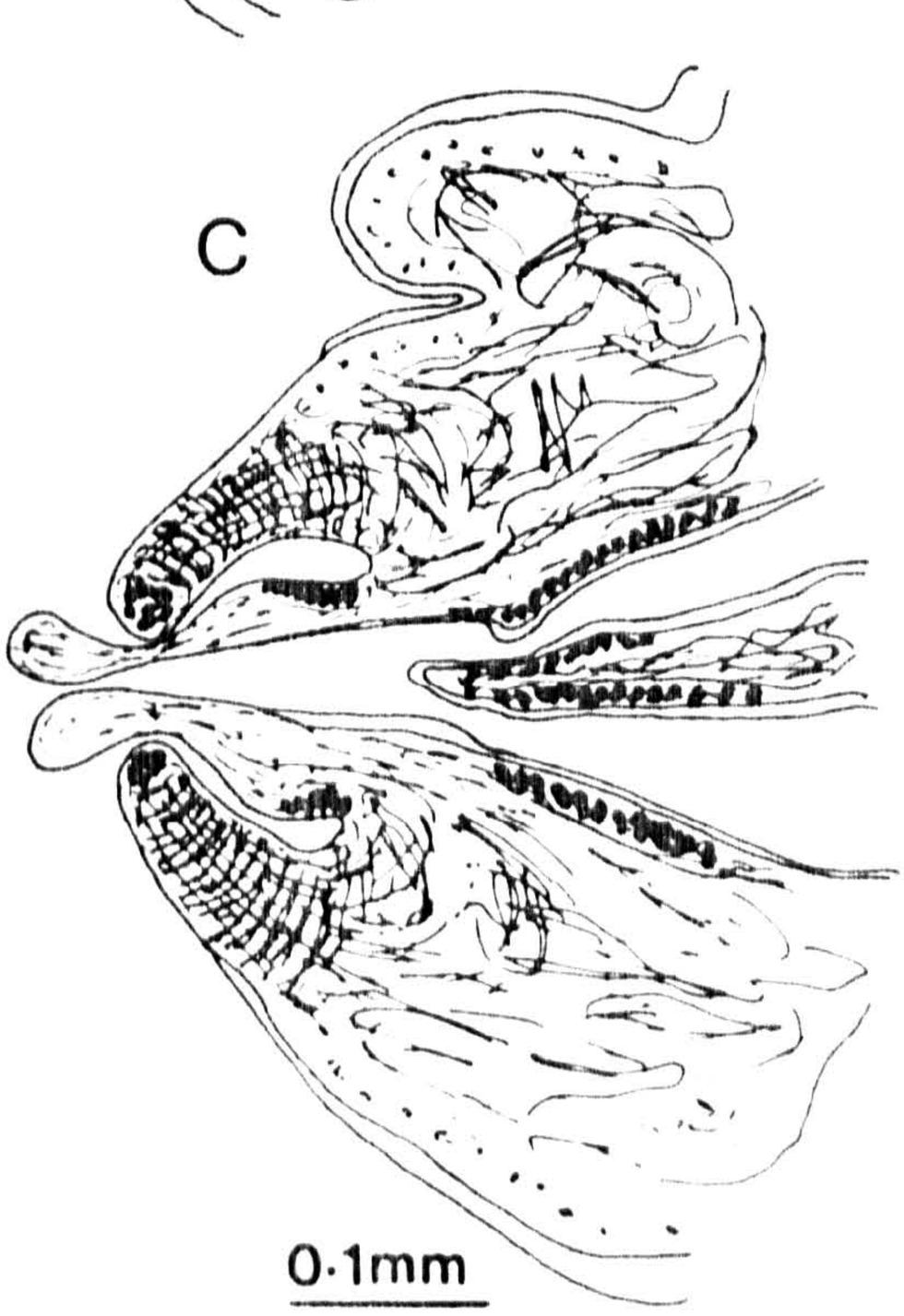
Types of terminal genitalium (vi)

(median sagittal section)

a - d. Microbothrium type (Näsmark, 1937) at various degrees of relaxation.


a
0·2mm


b
0·1mm


c
0·1mm

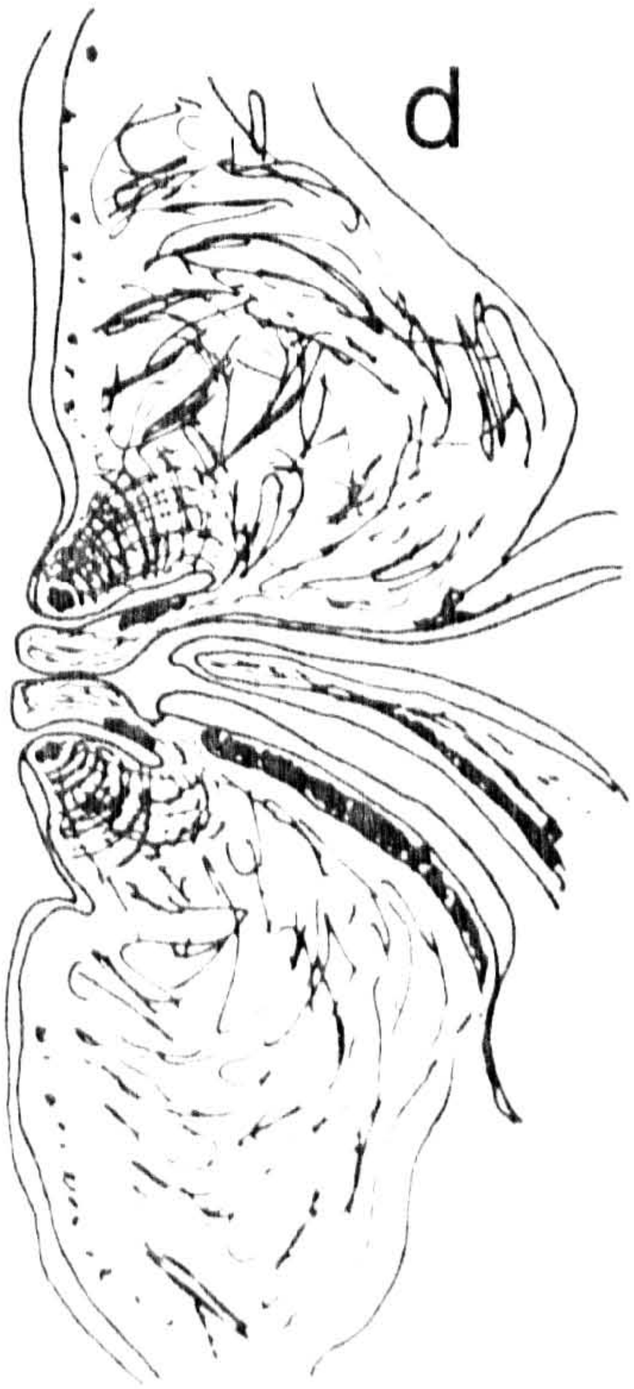

d
0·2 mm

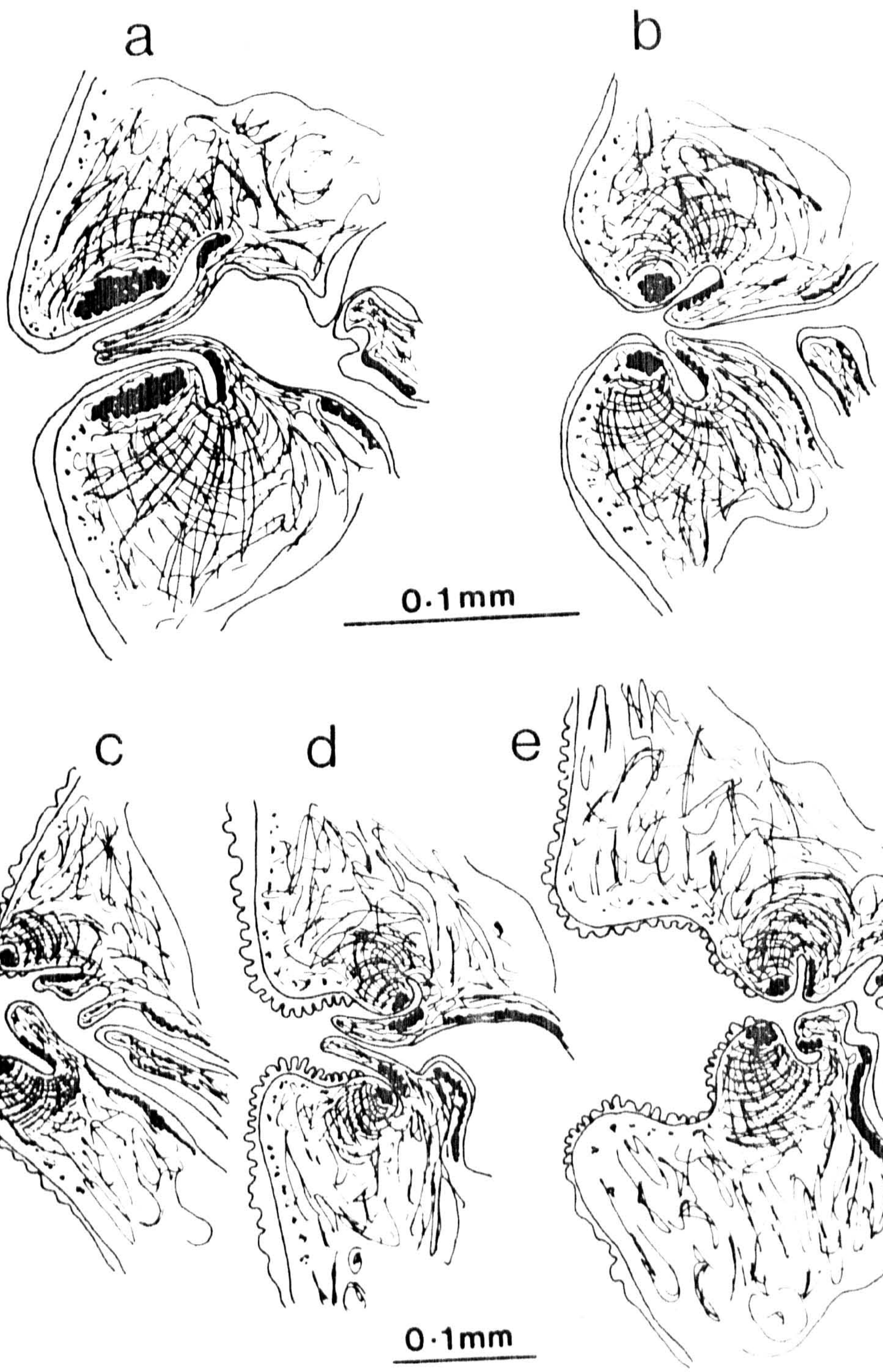
FIGURE 27

Types of terminal genitalium (vii)

(median sagittal section)

a - b. Scoliocoelium type (Näsmark, 1937)

c - e. Papillogenitalis type (Eduardo, 1980a) at various degrees of relaxation. Note presence of tegumental papillae on the surface of the genital fold.


a
b
0·1mm
c
d
e
0·1mm

ventral fold and ventral atrium may be formed when the genital fold and genital papilla are strongly retracted but are lost when these are normally relaxed.

11. Dawesi type (new type), Fig. 28a-b

Characterized by the presence of a compact and round to oval shaped genital sphincter and the absence of a sphincter papilla. Radial fibres moderately developed. Ventral fold and ventral atrium absent.

Gupta (1958b) when describing Ceylonocotyle dawesi (now Orthocoelium dawesi) illustrated this type but gave no name for it.

12. Ichikawai type (Näsmark, 1937), Fig. 28c-d

Genital fold well developed; genital sphincter absent; genital papilla well developed, thick and broad; sphincter papilla well developed. Radial musculature well developed. Ventral fold and ventral atrium absent.

13. Stephanopharynx type (Näsmark, 1937), Fig. 29a

Resembles the ichikawai type in the absence of a genital sphincter and the presence of a thick and well developed genital papilla and a well developed sphincter papilla but differs from it by the presence of large tegumental papillae on the surface of the genital fold. Radial fibres well developed. Ventral fold and ventral atrium absent.

14. Liorchis type (Näsmark, 1937), Fig. 29b

The wall of the whole structure has only few muscular fibres. Genital fold moderately developed; genital sphincter absent; genital papilla short;sphincter papilla weakly developed but distinct. Ventral fold and ventral atrium absent.

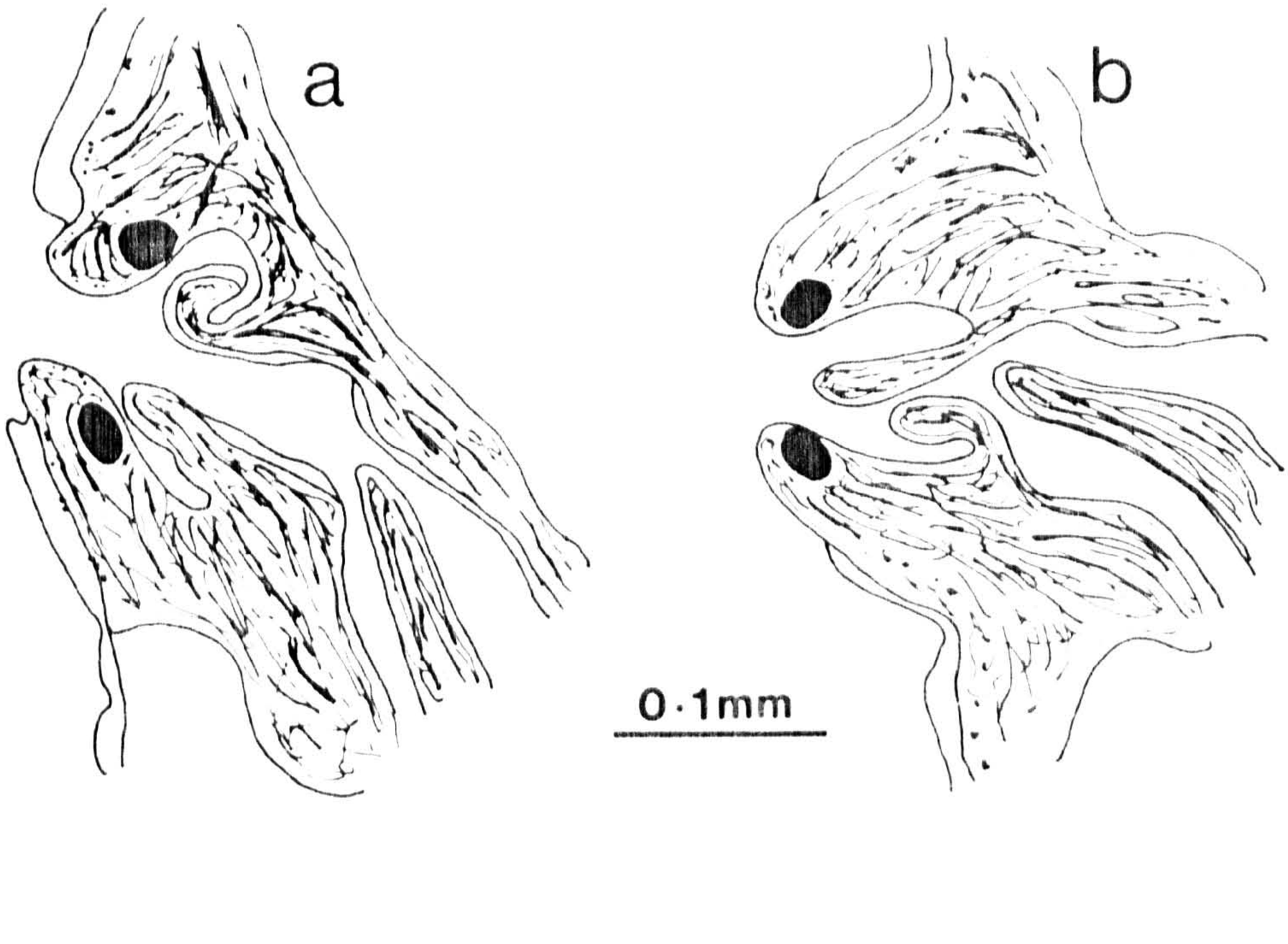
FIGURE 28

Types of terminal genitalium (viii)

(median sagittal section)

a - b. Dawesi type (new type)

c - d. Ichikawai type (Näsmark, 1937)


a
b
0·1mm

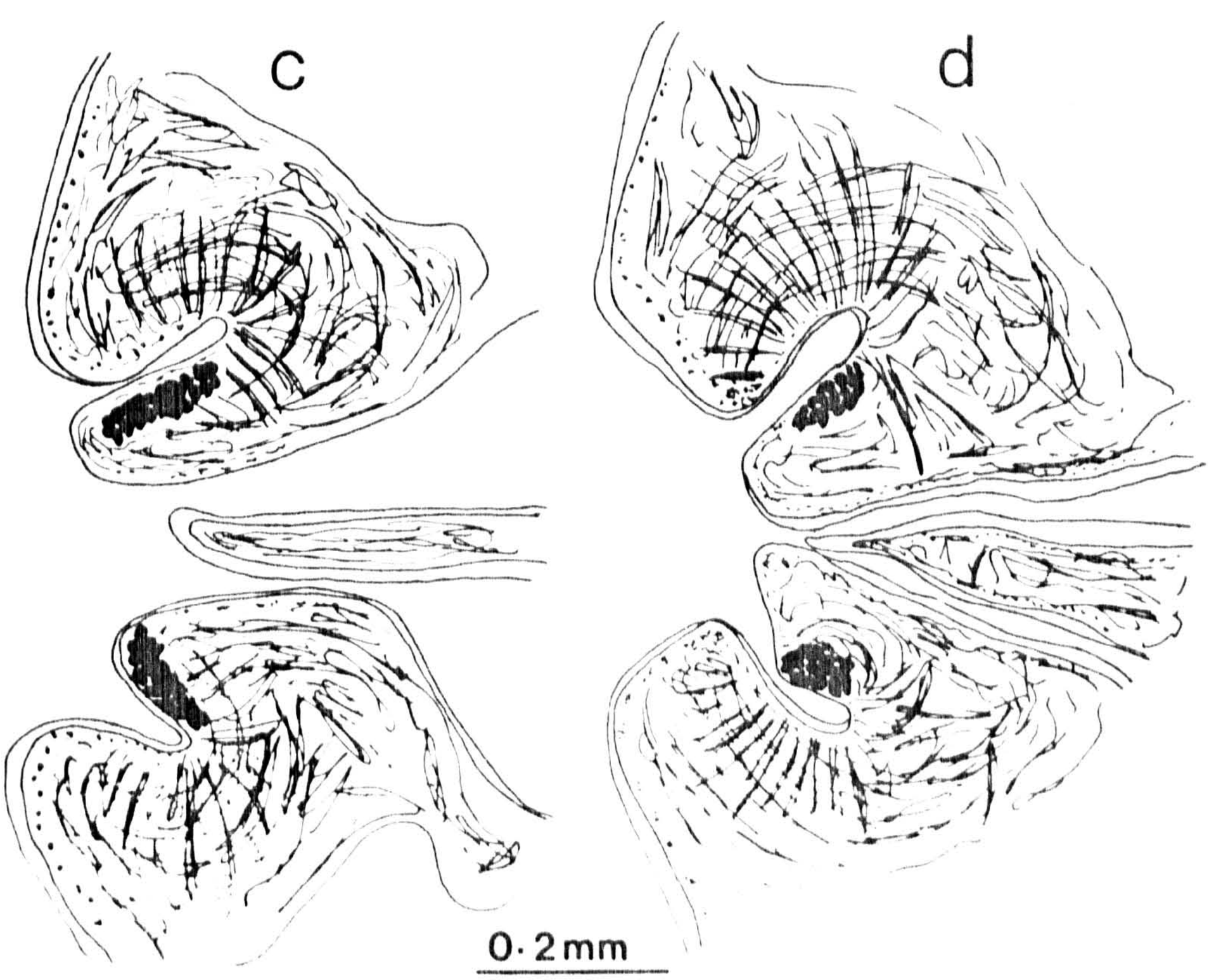

c
d
0·2mm

FIGURE 29

Types of terminal genitalium (ix)

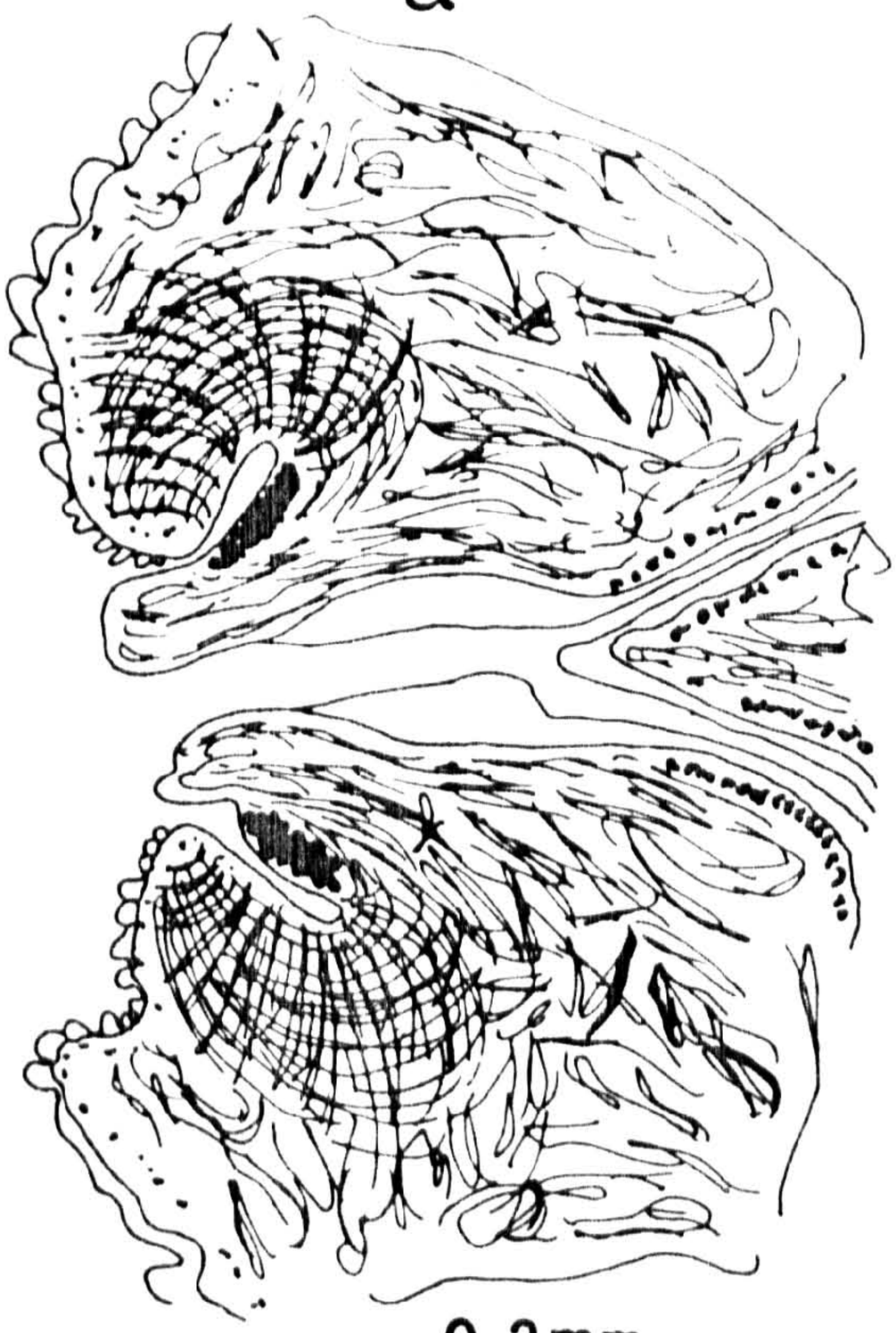
(median sagittal section)

a. Stephanopharynx type (Näsmark, 1937)

b. Liorchis type (Näsmark, 1937)

c - d. Explanatum type (Näsmark, 1937)

a



0·2mm

b

0·1mm

c

0·1mm

d

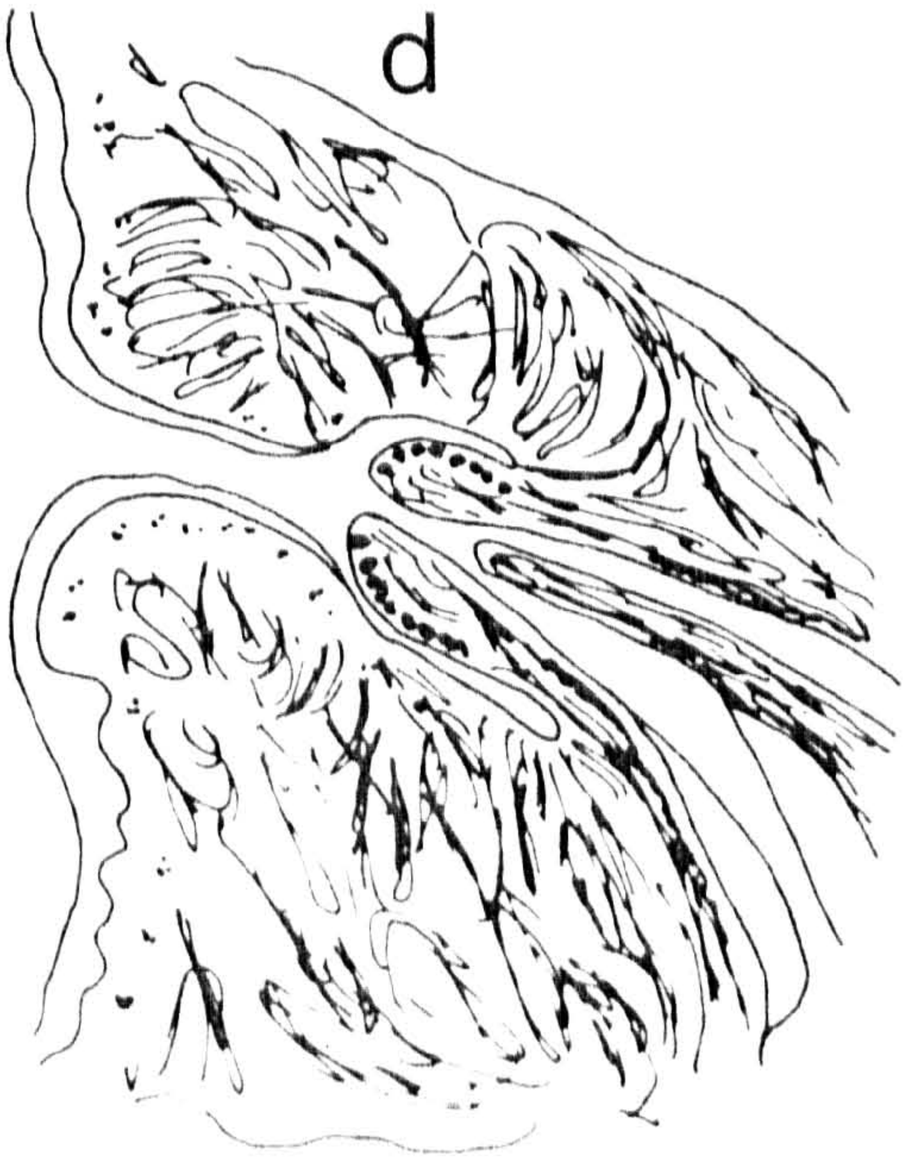


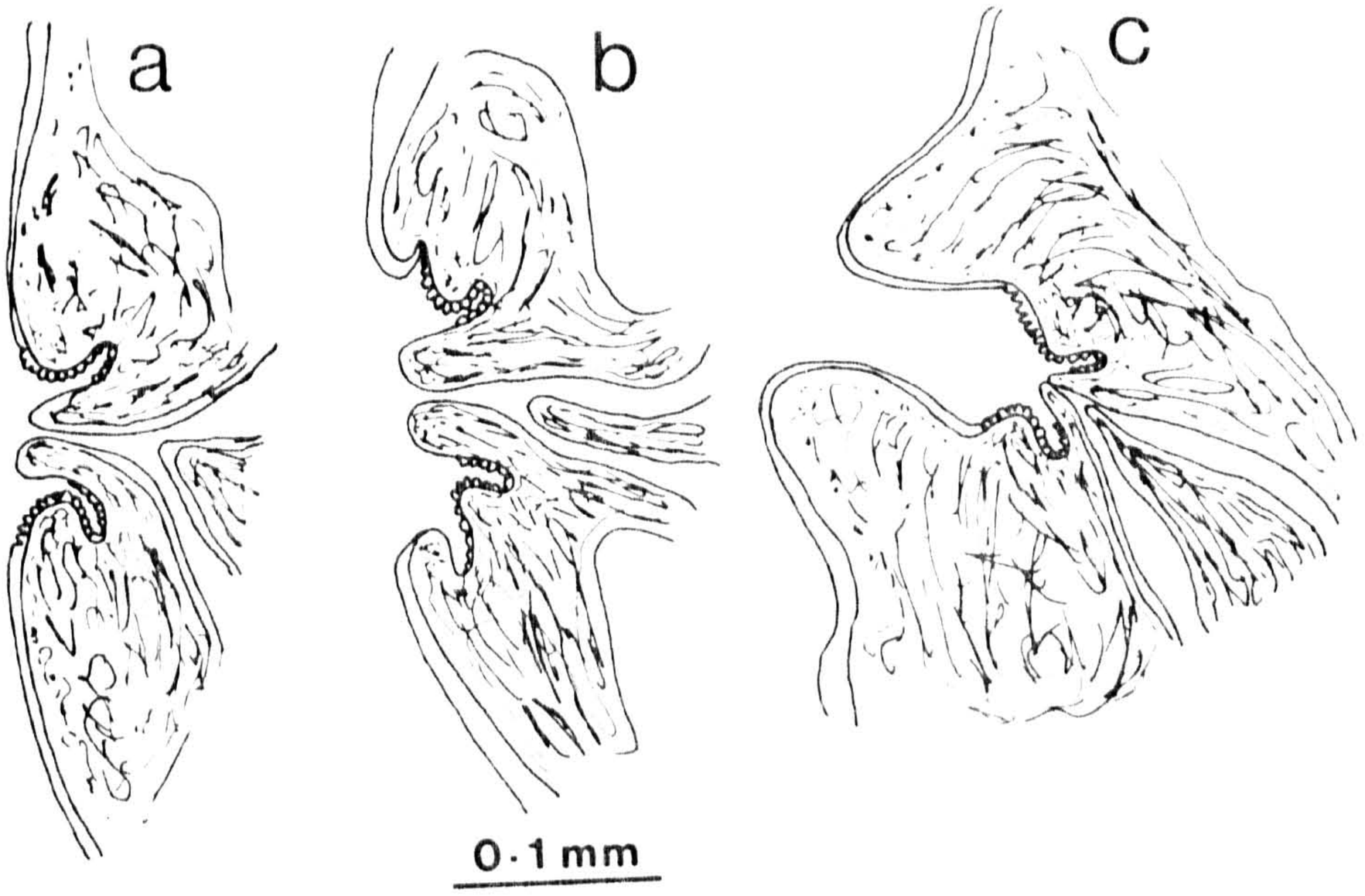
FIGURE 30

Types of terminal genitalium (x)

(median sagittal section)

a - c. Parvipapillatum type (new type)

d - e. Epiclitum type (Näsmark, 1937)


a
b
c
0·1 mm

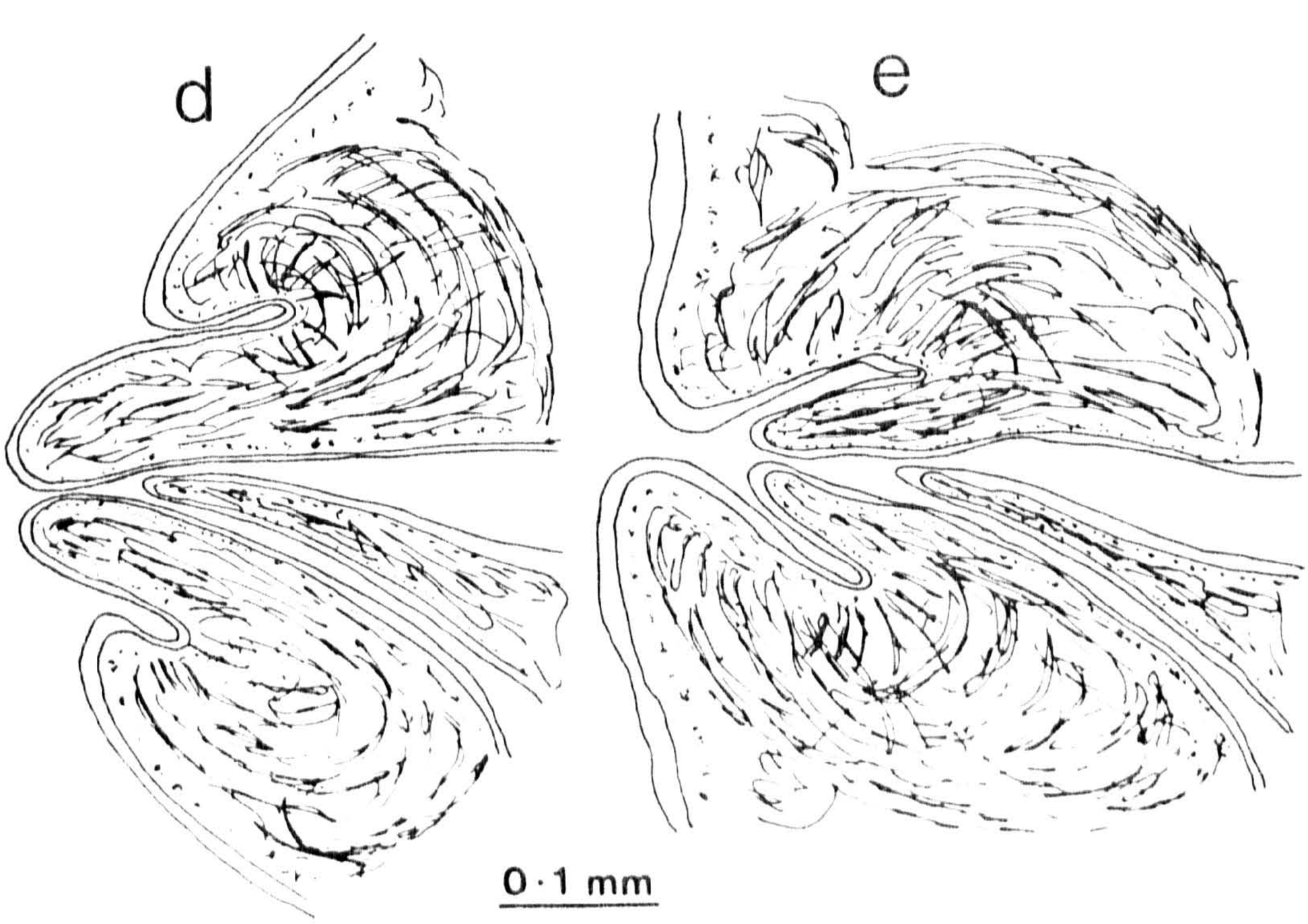
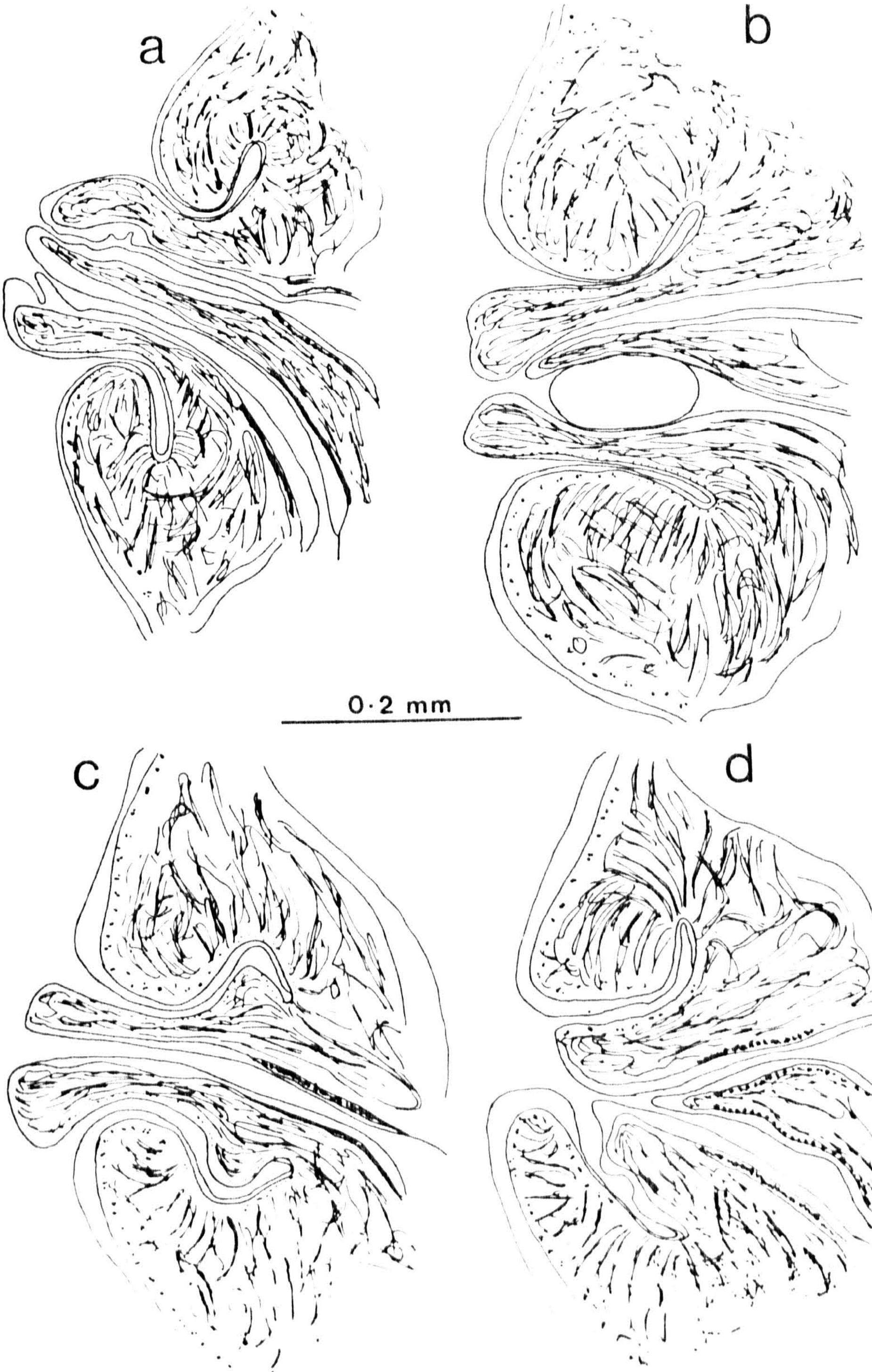

d
e
0·1 mm

FIGURE 31

Types of terminal genitalium (xi)

(median sagittal section)

a - d. Leydeni type (new type) at various degrees of relaxation.


a
b
0·2 mm
c
d

developed. Ventral fold and ventral atrium absent.

Näsmark (1937) when defining the epiclitum type referred Paramphistomum epiclitum and P. leydeni to it and the type was illustrated using the latter species. Re-examination of Nasmark's material as well as new materials of both species revealed that their terminal genitalium are not identical and they are separately defined and illustrated here accordingly.

19. Gracile type (Näsmark, 1937), Fig. 32a-d

Characterized by the presence of only few radial musculature and the absence of sphincters and other circular muscle fibres. Genital papilla of various forms, moderately to weakly developed. Ventral fold and ventral atrium absent.

20. Cotylophoron type (Näsmark, 1937), Fig. 33a-c

Characterized by the wall of the whole terminal structure which is developed into a sucker and is well marked off from the surrounding parenchyma. Genital papilla usually slender; genital sphincter and sphincter papilla absent. Radial fibres strongly developed. True ventral fold and ventral atrium absent but sometimes may be formed artificially when the genital sucker is strongly contracted.

21. Schistocotyle type (Sey and Graber, 1979a), Fig. 33d

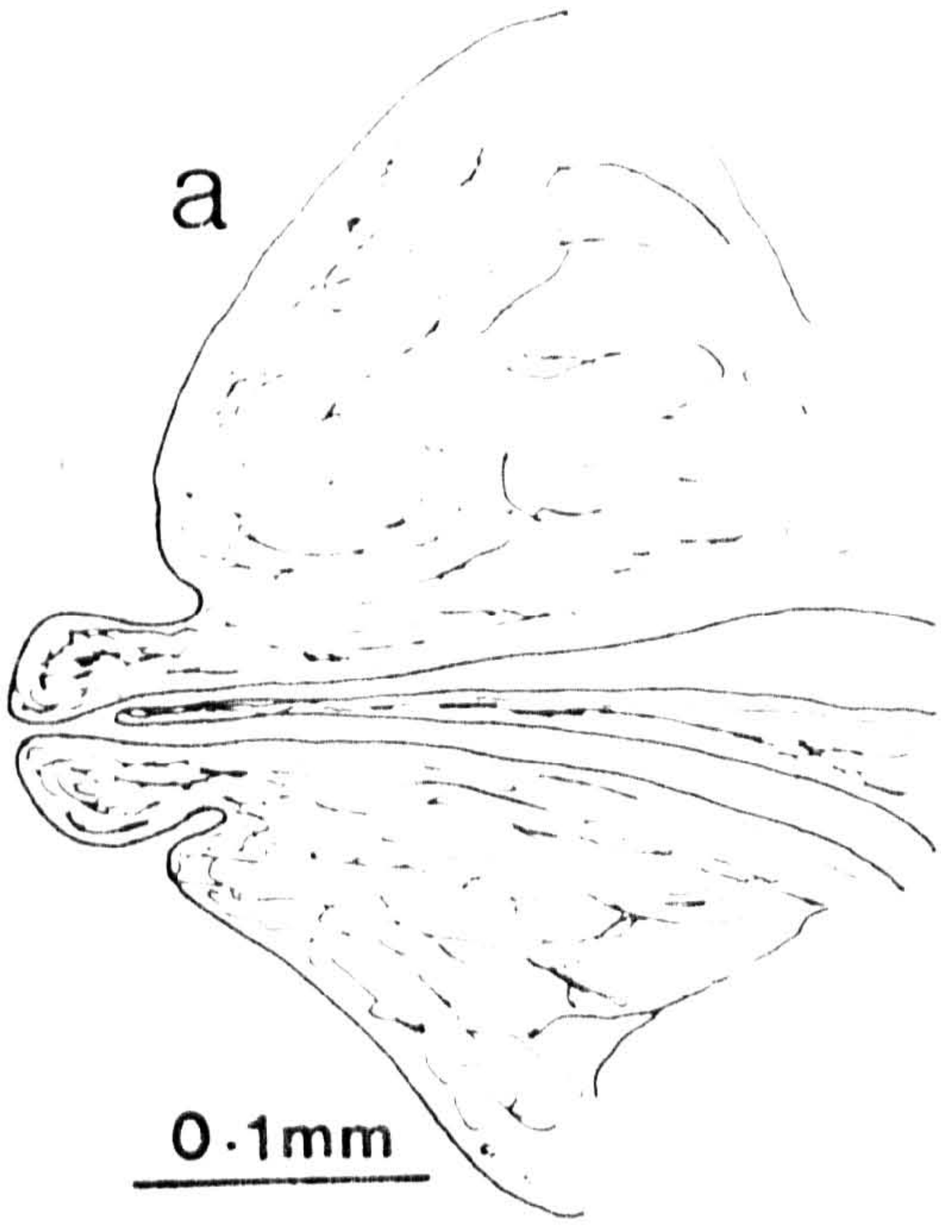
Resembles the preceeding type in the presence of a genital sucker but differs from it in the presence of strongly developed circular muscle units in the rim of the sucker forming a strong sphincter. Genital papilla thick and broad; sphincter papilla absent. Radial fibres strongly developed. Ventral fold and ventral atrium absent.

FIGURE 32

Types of terminal genitalium (xii)

(median sagittal section)

a - d. Gracile type (Näsmark, 1937) at various degrees of relaxation.


a
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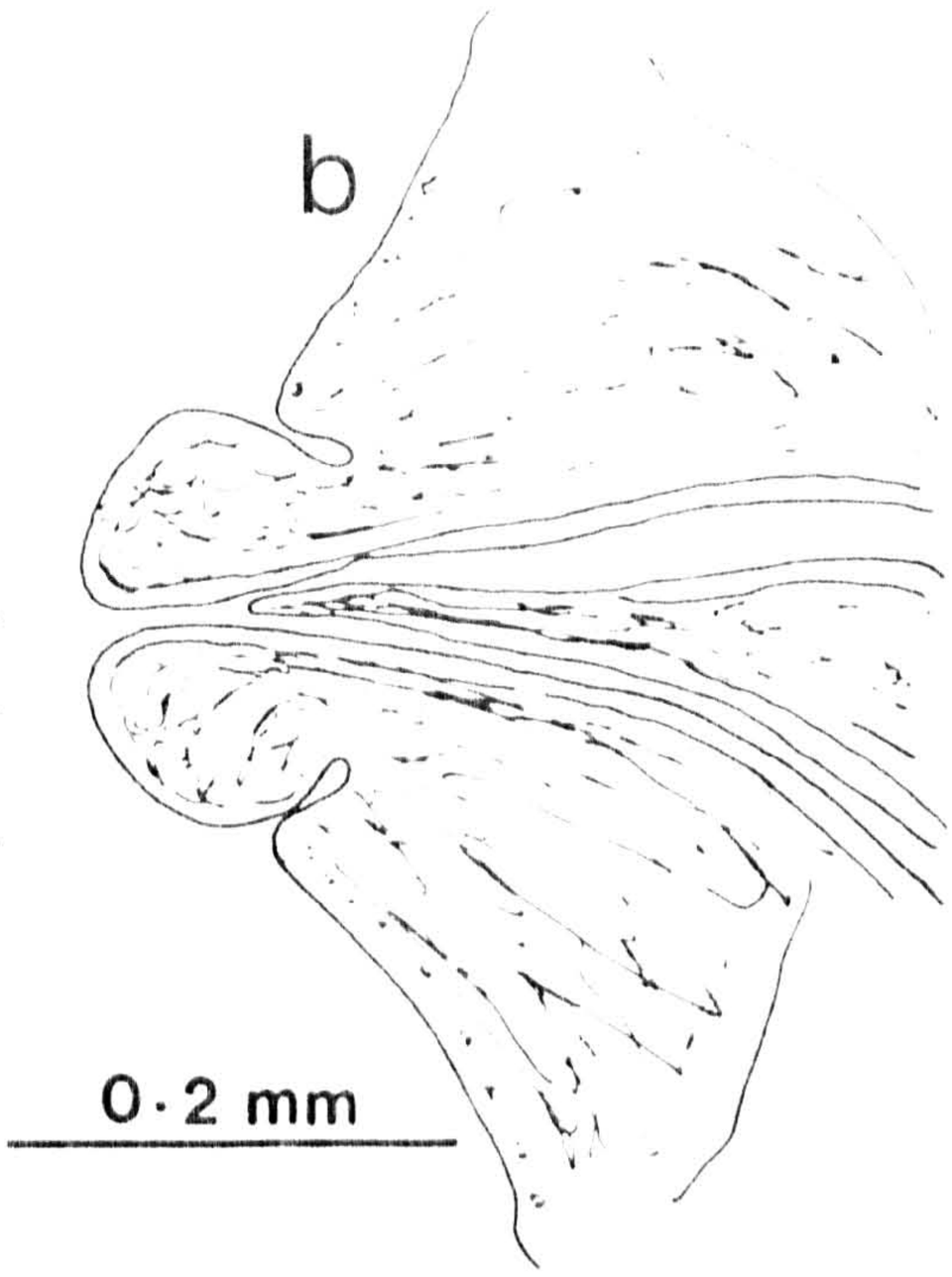
b
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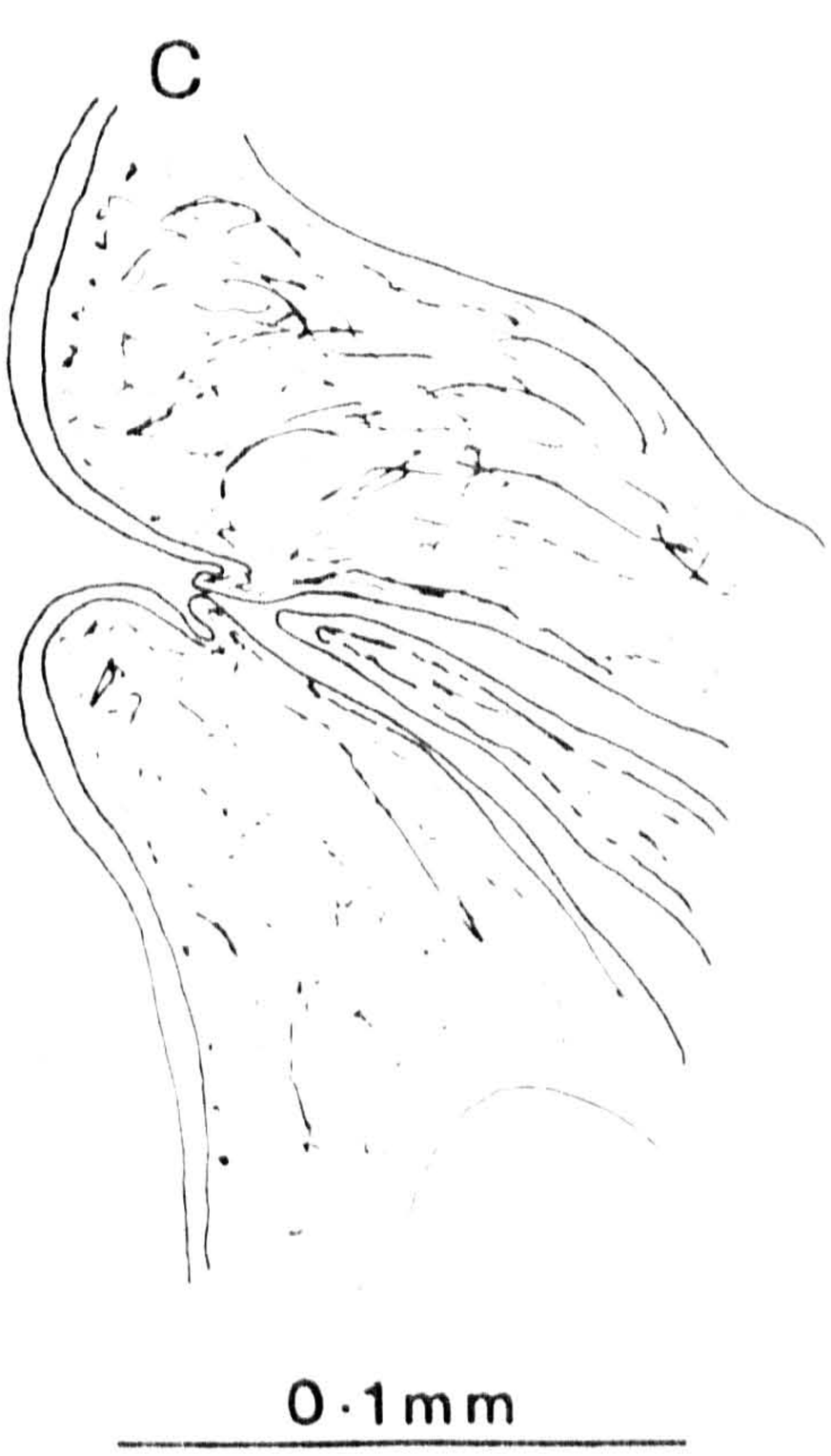

c
0·1mm


d
0·1 mm

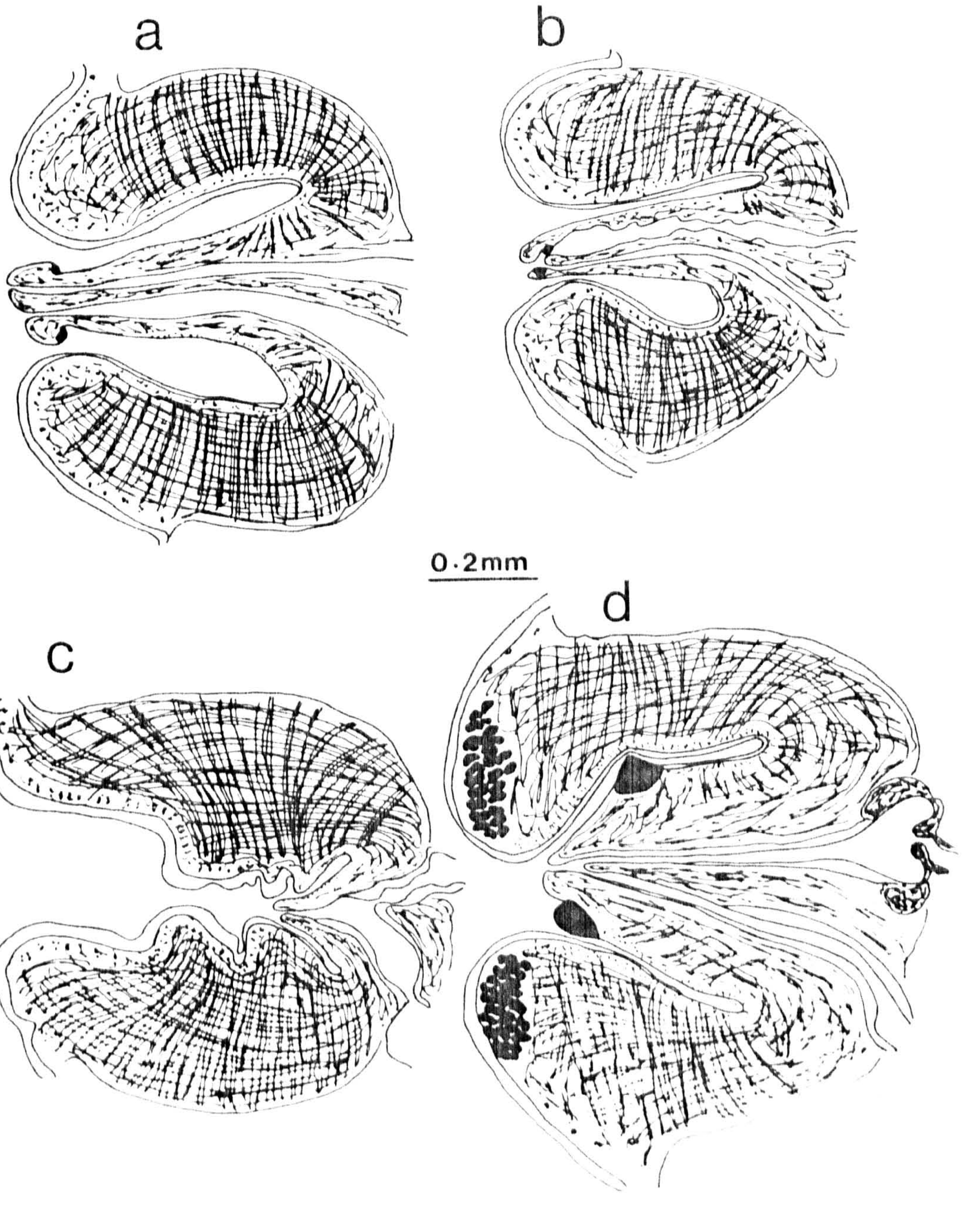
FIGURE 33

Types of terminal genitalium (xiii)

(median sagittal section)

a - c. Cotylophoron type (Näsmark, 1937) at various degrees of relaxation.

d. Schistocotyle type (Sey and Graber, 1979a)


a
b
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c
d

Näsmark (1937) mentioned that Taxorchis schistocotyle has a genital atrium surrounded by a sucker which is provided with a sphincter but gave no name for it. Sey and Graber (1979a) observed the same type in their material of Cotylophoron macrosphinctris and gave the name schistocotyle for it.

22. Balanorchis type (new type), Fig. 34

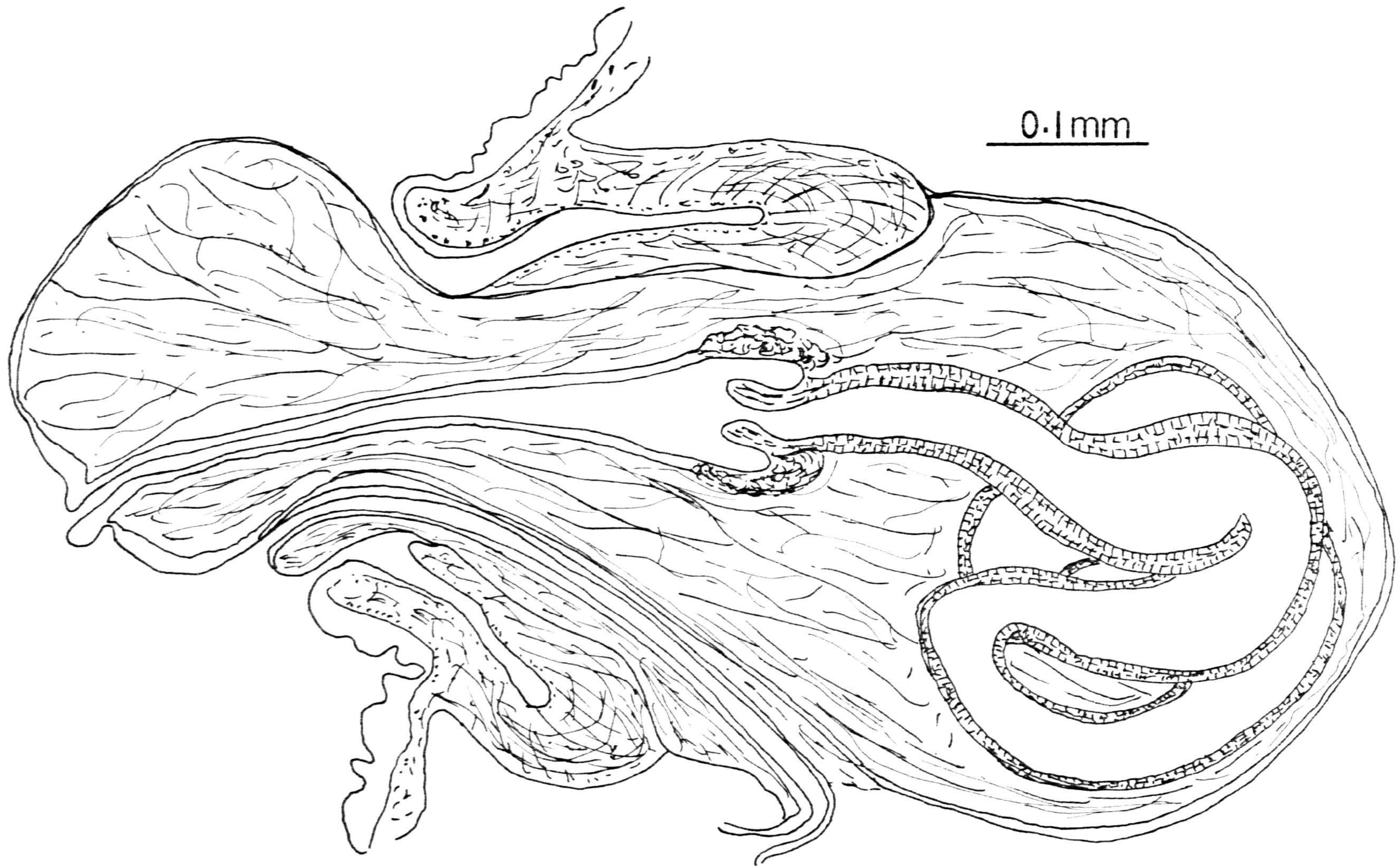
Characterized by the presence of a cirrus pouch which is protrusible to the outside of the body surface. Because of this, it could easily be mistaken for a genital papilla which is absent in this type. Genital fold small; sphincters absent.

FIGURE 34

Types of terminal genitalium (xiv)

(median sagittal section)

Balanorchis type (new type), note protrusible cirrus pouch.


0.1mm

Key to the types of terminal genitalium observed among the different species examined in this work

1. Cirrus pouch present and protrusible; genital papilla absent - Balanorchis

   cirrus pouch absent; genital papilla present - - - - - - - - - 2

2. Genital sucker present - 3

   Genital sucker absent - 4

3. Genital sphincter present; genital papilla usually broad - Schistocotyle

   Genital sphincter absent; genital papilla usually slender - Cotylophoron

4. True ventral atrium present and enormous - - - - - Bothriophoron

   True ventral atrium absent - - - - - - - - - - - - - - - - - - 5

5. Genital sphincter and sphincter papilla present - - - - - - - - 6

   Genital sphincter present, round to oval in shape; sphincter papilla absent - Dawesi

   Genital sphincter absent; sphincter papilla present - - - - - 13

   Genital sphincter and sphincter papilla absent - - - - - - - - 16

6. Whole terminal structure enormous - - - - - - - - Gigantocotyle

   Whole terminal structure not enormous - - - - - - - - - - - - 7

7. Sphincter papilla extensive joining the genital sphincter - Streptocoelium

   Sphincter papilla not extensive, not joining the genital sphincter - 8

8. Genital sphincter enormous, strong and compact - - - - - Clavula

   Genital sphincter not enormous, not compact but relatively well developed - 9

Genital sphincter slightly developed but distinct - - - - - 10

9. Sphincter papilla relatively well developed; genital papilla thick and broad; genital fold usually curves inwards with rim tapering to a point - - - - Orthocoelium

Sphincter papilla slightly developed, sometimes very weak; genital papilla slender and usually short; rim of genital fold rounded - - - - - - - - - - - - - Scoliocoelium

10. Genital pillar or column present and retractable - - - - - - 11

Genital pillar or column absent - - - - - - - - - - - - - - - 12

11. Tegumental papillae present on surface of the genital pillar or column - Raja

Tegumental papillae absent on surface of the genital pillar or column - - - - - - - - - - - - - - - - - - Calicophoron

12. Tegumental papillae present on surface of the genital fold - Papillogenitalis

Tegumental papillae absent on surface of the genital fold - Microbothrium

13. Genital papilla well developed, long and usually broad - - - 14

Genital papilla slightly developed and short - - - - - - - - - 15

14. Tegumental papillae present on surface of the genital fold - Stephanopharynx

Tegumental papillae absent on surface of the genital fold - Ichikawai

15. Whole terminal structure small; narrow canal leading to genital atrium present - - - - - - - - - - - - - - Explanatum

Whole terminal structure not small but moderate in size; canal leading to genital atrium absent - - - - - Liorchis

16. Wall of terminal genitalium circular in outline giving a sucker-like appearance - - - - - - - - - - - - - - - Epiclitum

    Wall of terminal genitalium not circular in outline - - - - 17

17. Radial fibres well developed; genital papilla thick and well developed - Leydeni

    Radial fibres and other musculature weakly developed or absent; genital papilla usually slender - - - - - - - - - 18

18. Tegumental papillae present on surface of genital fold and base of genital papilla - - - - - - - - - - Parvipapillatum

    Tegumental papillae absent on surface of genital fold and genital papilla - - - - - - - - - - - - - - - - - - Gracile

THE OESOPHAGUS

Many authors agree that the development of the musculature of the wall of the oesophagus is very important in specific diagnosis. The wall may be uniformly thin or very much thickened throughout its length or only the posterior end is thickened into a small sphincter or developed into a large muscular bulb. These have been employed as characters of specific value and this study confirms their usefulness. One aspect however has not been given attention, i.e. the lining of the internal surface of the oesophagus. The majority of the amphistome species have oesophagus lined by a hyaline layer throughout its length. However, there are few species where this type of lining does not hold true. Fukui (1929) observed that the oesophagus of Gastrothylax cobboldi (now Fischoederius cobboldi) has two types of lining, the anterior part lined by a "cuticular" layer and the posterior part by "ciliated" epithelium. Grétillat (1958) also observed the same types of lining in his specimens of Paramphistomum bothriophoron and regarded the part with hyaline lining the "pre-oesophageal organ" and the part with ciliated lining the main oesophagus. Because of this, he elevated Bothriophoron to full generic rank, thus regarding this character of generic value. Examination of specimens of the above species in the present study confirms the correctness of the above observations with respect to their oesophageal lining. Two species representing different genera were also found to have the above types of oesophageal lining. These are Calicophoron sukari and Gigantocotyle symmeri. This clearly indicates that oesophageal lining could not be taken into account as a character of generic value but only of specific value.

The different forms of the development of the wall musculature and types of lining of the internal surface of the oesophagus are illustrated in the accompanying microphotographs.

It is clear from the above discussion that no single morphological or histological character alone is sufficient enough to differentiate genera and species and that specific diagnosis always requires histological examination. Combinations of characters are more reliable in the taxonomy of the group. It also appears that tegumental papillae, their occurrence, distribution and types, are useful characters that can be employed to support other existing features in species differentiation. Although their use is limited because accurate observation can only be achieved by examination of suitably fixed specimens and under the scanning electron microscope, their value in the taxonomy of the group can no longer be disregarded. It is therefore necessary that any collection survey to be undertaken for the group should include proper preparation of fixation for scanning electron microscopy. Since the scanning electron microscope is becomming a standard feature in any taxonomic laboratory, specimens should also be examined by this method.

FIGURE 35

Various forms of the development of the wall musculature and types of lining of the internal surface of the oesophagus

a. Wall musculature relatively thin and more or less uniform throughout the whole length, internal surface lined by hyaline layer throughout the whole length (scale bar = 48 µm).

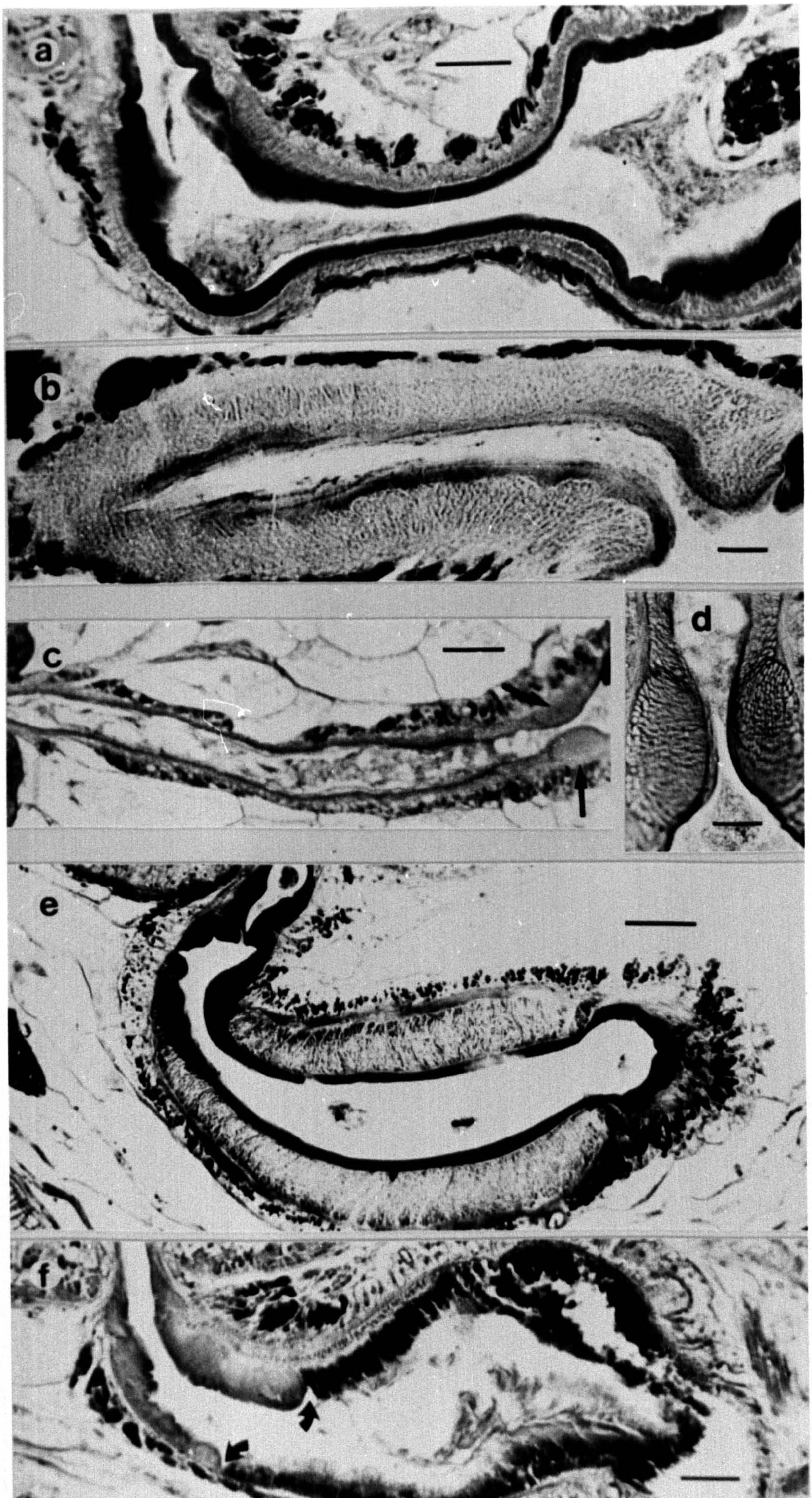
b. Wall musculature uniformly thickened and internal surface lined by hyaline layer throughout the length (scale bar = 25 µm).

c. Wall musculature thickened only in the posterior part forming a small posterior sphincter (indicated by arrows), internal surface lined by hyaline layer throughout the whole length (scale bar = 80 µm).

d. Closer view of posterior sphincter in Fig. c (scale bar = 22 µm).

e. Wall musculature developed into a muscular bulb, internal surface lined by a hyaline layer throughout the whole length (scale bar = 100 µm).

f. Wall musculature uniformly thin, internal surface lining consists of two types, anterior part lined by hyaline layer and posterior part by ciliated epithelium similar to that lining the caeca. Arrows indicate junction between the two linings (scale bar = 40 µm).


a
b
c
d
e
f

2. A DISCUSSION AND REVISION OF TEN GENERA OCCURRING IN RUMINANTS

Materials and Methods

Materials examined in this work were obtained from various sources. Majority of the specimens were from the collection of Dr. J.A. Dinnik, the late Dr. P.L. LeRoux, the London School of Hygiene and Tropical Medicine and the Commonwealth Institute of Helminthology. The first three collections are now housed in the latter institution.

Materials were also examined from the reference collection of the British Museum (Natural History); London School of Hygiene and Tropical Medicine; Commonwealth Institute of Helminthology; Naturhistoriska riksmuseet, Stockholm Sweden; Musée Royal de l'Afrique Centrale, Tervuren, Belgium; Instituto Oswaldo Cruz, Rio de Janeiro, Brazil; Institut für Parasitologie und Allgemeine Zoologie der Veterinärmedizinischen Universität Wien, Austria and the Onderstepoort Veterinary Research Institute, Transvaal, Republic of South Africa.

Additional materials were obtained from numerous individuals in various parts of the world who kindly provided specimens on request and they are listed under materials examined for each species and under acknowledgements. Specimens from the Philippines are the author's own collection.

Type specimens were examined from the collection of the following institutions: Naturhistoriska riksmuseet, Stockholm, Sweden; Musée Royal de l'Afrique Centrale, Tervuren, Belgium; Museum für Naturkunde (Bereich Zoologisches Museum) an der Alexander von Humboldt Universität zu Berlin, German Democratic Republic; British Museum (Natural History) London; Muséum d'Histoire Naturelle

Genève, Switzerland; United States National Parasite Collection, USDA, Beltsville, Maryland, U.S.A.; American Museum of Natural History, New York, U.S.A.; London School of Hygiene and Tropical Medicine, London and the Commonwealth Institute of Helminthology, St. Albans, United Kingdom.

Flattened specimens of amphistomes have no value in taxonomic study. Because of the conical shape and thickness of the body, flattening causes great distortion of shape of the body and the arrangements and shapes of the various organs. Furthermore, specific identification largely depends on examination of histological features which can only be demonstrated in sections. Specimens were therefore examined as sections both as hand thick and microscopic sections in the frontal, sagittal and transverse planes. In cases where the number of specimens is limited, sections were made only in the sagittal plane. Shape and form of each specimen were carefully noted before processing for sectioning. Where sufficient number and suitably fixed materials of a particular species were available, representative specimens were also processed for scanning electron microscopy of the tegumental surfaces.

Staining specimens for and the technique of hand cutting

Specimens received were already fixed either in formalin (10 per cent) or in alcohol (70 per cent). Those fixed in the former were first washed in running water and those fixed in the latter were gradually hydrated to water. Specimens were then placed overnight in aceto-alum-carmine stain, destained in aqueous acid solution (1 per cent HCl) to the desired colour, gradually

dehydrated in increasing grades of alcohol and cleared in clove oil. It was observed in the present study that when whole specimens were placed in the staining solution, even in prolonged overnight staining, complete penetration by the stain was not achieved because of the thickness of the worms resulting in specimens with the central parts remaining unstained. This is particularly true in formalin-fixed specimens where the hardened tissue is not easily penetrated by the staining solution. However, this was overcome by cutting each specimen into two equal halves before placing in the stain. To avoid incorrect pairing of halves later, only those cut in different planes (frontal, sagittal and transverse) were mixed together in the same staining solution. By this method, a very satisfactory result of stained specimens was achieved. Stained and cleared specimens were then further cut into thick sections following the technique of Dr. J.A. Dinnik (unpublished) but modified to produce fairly uniform sections. Instead of just holding the specimen between the thumb and index finger and cutting with a razor blade, a simple cutting stage was devised. This consists of a piece of glass slide and cover glasses. Equal numbers of cover glasses are glued on each end on one side of the glass slide using Canada balsam (see illustrations in Fig. 36). Depending on the thickness of the section desired, one can pile one or more cover glasses. Since the thickness of each cover glass is known, the thickness of the section made can easily be calculated. Complete drying of the Canada balsam is essential so that the cover glasses are permanently glued on the glass slide. The cleared specimen which was already cut into equal halves before staining is placed on the center of the cutting stage between the pile of

FIGURE 36

Schematic diagram showing the components of a cutting stage and their arrangements, the position of the cutting blade and the specimen on the stage in the preparation of hand thick sections as well as the proper arrangement of sections on glass slides for permanent mounting.

a. Top view of cutting stage showing positions of cutting blade and specimen.

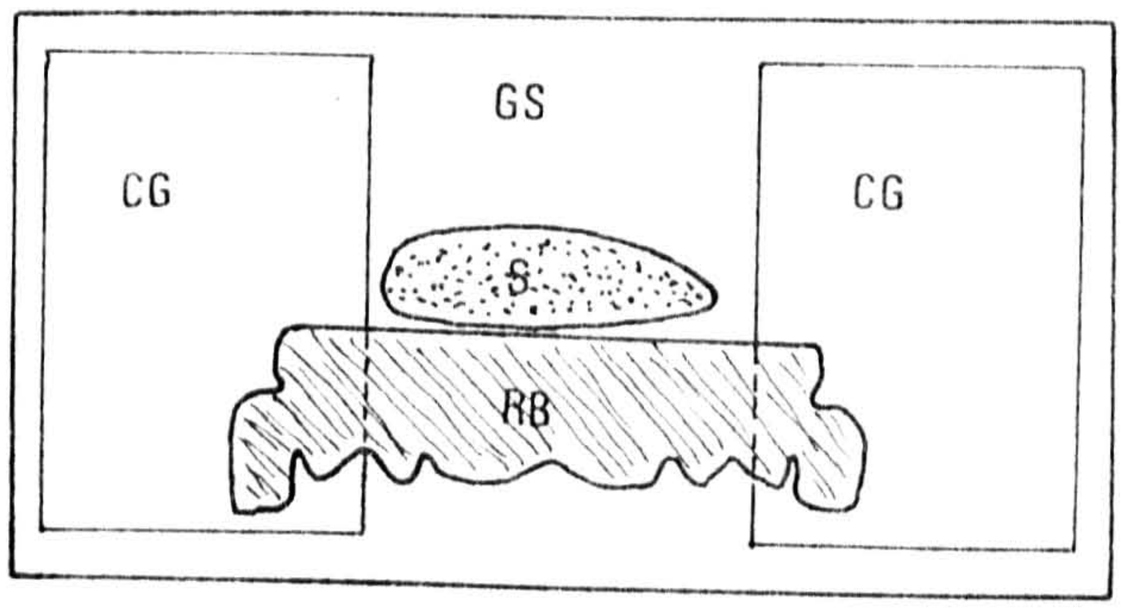
b. Side view of the same.

c. Showing proper arrangement of sagittally cut thick sections.

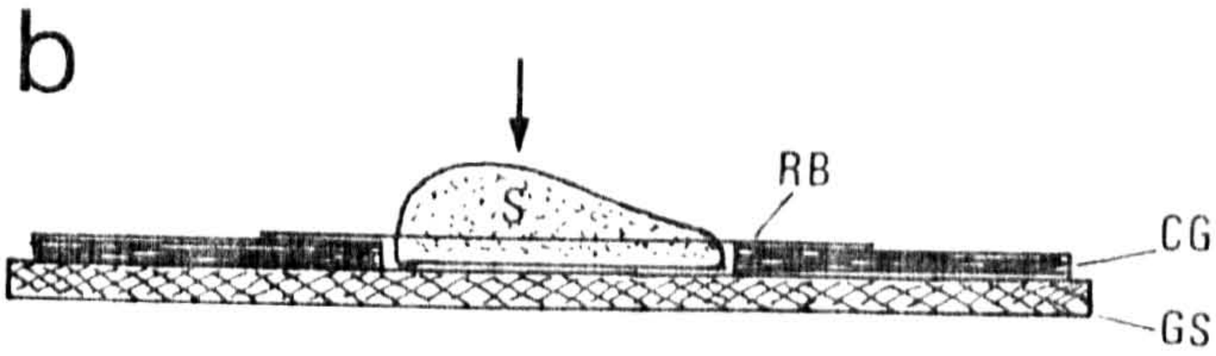
Key to Abbreviations:

CG - cover glass
GS - glass slide
LSL - lateral sagittal section, left side of specimen.
LSR - lateral sagittal section, right side of specimen.
MS - median sagittal section
RB - razor blade
S - specimen

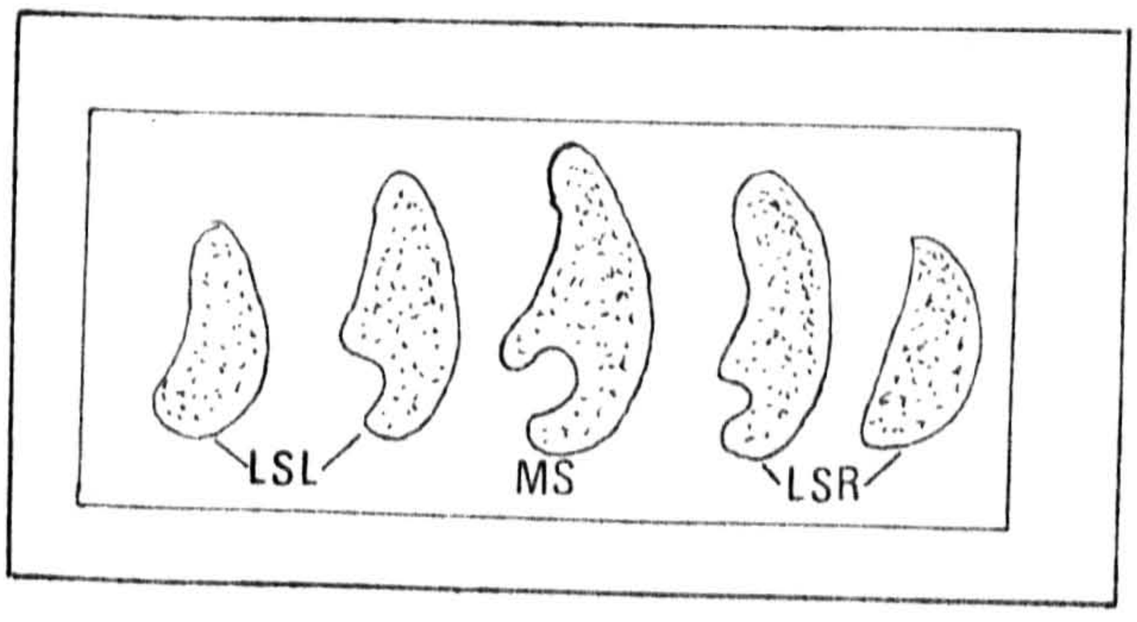
a



b



C



cover glasses with the cut surface on the stage. Holding the specimen firm on the stage by exerting an index finger or thumb pressure, each thick section was made by sliding through it a razor blade with the ends of the blade resting on the pile of cover glasses. The sections were placed again in clove oil before they were arranged on glass slides in the proper sequence and mounted in Canada balsam.

Processing specimens for microscopic sectioning and staining

Microscopic sections were prepared following the standard paraffin method. Sections were cut 8 to 12 µm using a sliding microtome (MSE), stained in Delafield's haematoxylin, counter-stained in eosin and mounted in Canada balsam.

Sections were examined under Wild research (M11) and stereo (M5) microscopes and drawings were made with the aid of drawing tubes attached to these microscopes.

Processing specimens for scanning electron microscopy

Since specimens received were already fixed, only those which appeared in good condition after careful examination under the stereomicroscope were used. Specific identity was first established by examination of sectioned materials and only those lots which proved to consist only of a single species were processed. Specimens were first washed carefully in distilled water with few drops of detergent solution by shaking gently to dislodge any attached debris. These were then gradually dehydrated in increasing grades of alcohol, critically point dried using a Polaron critical point dryer, mounted on metal stubs, coated with gold using a

Polaron E5100 SEM coating unit and examined under an ISI-60 (International Scientific Instruments) scanning electron microscope unit.

Revision of the genus Paramphistomum Fischoeder, 1901

INTRODUCTION

The genus Paramphistomum was proposed by Fischoeder (1901, 1902, 1903) to replace the name Amphistoma Rudolphi, 1809 in part, which was, as he pointed out, in reality a synonym of a previously valid genus Strigea Abildgaard, 1790. Under the genus, he assigned and redescribed Paramphistomum cervi (Zeder, 1790) and P. bothriophoron (Braun, 1892) as new combinations and designated the former as the type species of the genus. He also described nine new species namely: Paramphistomum liorchis, P. bathycotyle, P. gracile, P. orthocoelium, P. dicranocoelium, P. streptocoelium, P. microbothrium, P. calicophorum and P. cotylophorum. He divided the genus into three groups of species based on the presence or absence of a crossing between Laurer's canal and excretory vesicle and the development of the pars musculosa. In 1904, he added P. scoliocoelium and P. epiclitum as new species and redescribed P. explanatum (Creplin, 1847) as a new comibation from new material.

Stiles and Goldberger (1910) added the following from ruminants as new species: P. papilligerum, P. cauliorchis, P. crassum, P. papillosum, P. indicum, P. fraternum, P. parvipapillatum, P. shipleyi and P. siamense. They removed P. cotylophorum Fischoeder, 1901 from the genus on account of the presence of a genital sucker and erected the genus Cotylophoron for its reception. They subdivided the genus into four subgenera namely: Paramphistomum, Orthocoelium, Bothriophoron and Cauliorchis based on the presence of a ventral chamber in the genital atrium, whether Laurer's canal crosses the excretory vesicle or not and the size of the acetabulum.

However, four species were placed under an uncertain subgenus. Leiper in the same year (1910) described five new species from the hippopotamus namely: P. pisum, P. sellsi, P. minutum, P. wagandi and P. buxifrons. Based on new materials, he redescribed P. gigantocotyle (Brandes in Otto, 1896) as a new combination.

Faust (1920) described P. anisocotylea from cattle and carabao in the Philippines. Fukui (1922a, 1922b, 1922c) added to the genus P. ijimai, P. gotoi and P. ichikawai, all from ruminants in Japan. In 1929, he described P. formosanum from Bos chinensis in Formosa.

Maplestone (1923) relegated most of the above species to synonymy without examining type specimens. He accepted only eight species valid as follows: P. cervi, P. liorchis, P. pisum, P. gigantocotyle, P. explanatum, P. buxifrons, P. wagandi and P. orthocoelium. Railliet (1924) gave the names P. birmense and P. microon to specimens reported by Evans and Rennie (1908) from the bile duct and caecum respectively of ox in Burma.

Fukui (1929) changed Paramphistomum to Paramphistoma without giving any reason. He accepted most of Maplestone's synonymies but regarded P. pisum as a synonym of P. cervi and P. bothriophoron as distinct and valid. He reduced the genus Cotylophoron Stiles and Goldberger, 1910 to subgeneric status and erected three other subgenera under the genus Paramphistoma namely: Paramphistoma, Buxifrons and Explanatum on the basis of the presence or absence of genital sucker and arrangement of the testes. Stunkard (1929), Sprehn (1932), Travassos (1934), Bhalerao (1935), Neveu-Lemaire (1936) and Dawes (1936, 1956) simply followed most of Maplestone's synonymies withoug re-examining type specimens. Travassos (1934) upheld the genus Cotylophoron Stiles and Goldberger, 1910 while

Dawes (1936) concured with Fukui (1929) in rejecting it and he accepted no subgeneric division of the genus Paramphistomum.

Holl (1929) described Paramphistomum stunkardi from fishes (Eupomotis gibbosus and Chaenobrythus gulosus) but it is now the type species of the genus Pisciamphistoma Yamaguti, 1953. Hsu (1935) described P. chinensis from cows in China but the species is regarded by Yamaguti (1971) as a synonym of Orthocoelium orthocoelium (Fischoeder, 1901).

Näsmark (1937) revised the family Paramphistomidae Fischoeder, 1901 utilizing histological features, particularly of the pharynx, acetabulum and genital atrium as seen in median sagittal section as characters of taxonomic value. He recognised the genus Cotylophoron Stiles and Goldberger, 1910 and resurrected most species of the genus Paramphistomum previously considered not valid. He removed some species from the genus Paramphistomum and erected new genera to contain them as follows: Calicophoron, Gigantocotyle, Nilocotyle, Macropharynx, Ugandocotyle and Buxifrons. Under the genus Paramphistomum, he retained and redescribed the following species: P. cervi, P. epiclitum, P. microbothrium, P. ichikawai, P. bothriophoron, P. papilligerum, P. liorchis and P. gotoi. He also described two new species, P. leydeni and P. clavula.

Bhalerao (1937) described P. maplestonei and P. cuonum from Hyelaphus porcinus and Cuon dukhenensis respectively in India. Yamaguti (1958) however removed both species and erected two new genera, Paramphistomoides and Pseudoparamphistoma respectively for their reception. Mukherjee and Chauhan (1965) rejected Yamaguti's genera and moved instead the two species to the genus Ceylonocotyle Näsmark, 1937 (now a junior synonym of Orthocoelium Stiles and

Goldberger, (1910) in new combinations. Yamaguti (1971) retained the two species under the genera he established in 1958.

Popova (1937) described P. skrjabini from cattle in Russia but Davydova (1959) synonymised the species with Calicophoron calicophorum (Fischoeder, 1901) Näsmark, 1937. On the other hand, Yamaguti (1971) listed it as a separate species under the genus Paramphistomum.

Johnson (1939) described P. magnum from a cow in India but it is now the type and only species of the genus Johnsonitrema Yamaguti, 1958 in the family Gastrothylacidae Stiles and Goldberger, 1910. Price and McIntosh (1944) briefly described P. microbothrioides as new species from cattle in the U.S.A. Tandon (1955a) described P. spinecephalus from Bubalus bubalis in India. However, Mukherjee (1960) as cited by Mukherjee and Chauhan (1965) transfered the species to the genus Ceylonocotyle Näsmark, 1937 in a new combination because Laurer's canal does not cross the excretory vesicle or duct. Yamaguti (1971) retained the species in the genus Paramphistomum with a note "generic status sub judice".

Willmott (1950b) described P. hiberniae and P. scotiae from cattle in Ireland, the Netherlands and Scotland. Velichko (1966b) removed both species from the genus and erected the genus Liorchis to contain them. Sey (1974) rejected the genus Liorchis and doubted the validity of P. scotiae. He suggested that the species is either closely related to or identical with P. leydeni Näsmark, 1937. Kamburov (1976) concured with Sey (1974) in rejecting Liorchis and regarded both P. hiberniae and P. scotiae as synonyms of P. cervi. Odening, Bockhardt and Gräfner (1978) also regarded both species and P. leydeni as synonyms of P. cervi.

Price and McIntosh (1953) after re-examining the types of Cotylophoron indicum Stiles and Goldberger, 1910 came to the conclusion that the species belongs to the genus Paramphistomum. Since there is already a species by that name in the genus, they proposed the name Paramphistomum thapari for it. Velichko (1966a) re-examined the types of Ceylonocotyle petrovi Davydova, 1961 as well as examined new materials of that species and found out that it belongs to the genus Paramphistomum.

From ruminants in Africa, Dinnik (1954, 1961, 1962, 1964) described the following as new species: P. sukari, P. phillerouxi, P. daubneyi and P. sukumum. Grétillat (1958) elevated the subgenus Bothriophoron Stiles and Goldberger, 1910 to full generic rank, consequently P. bothriophoron is removed from the genus.

Recently, new species have been described and assigned to the genus namely: P. vangrembergeni Van Strydonck, 1970 from bovidae and Kobus sp. in the Belgian Congo (now Zaîre); P. malayi Lee and Lowe, 1971 from Bubalus bubalis in Malaysia; P. nica-brasilorum Velazquez-Maldonado, 1976 and P. julimarinorum Velazquez-Maldonado, 1976 both from Bos taurus in Brazil; P. bombayiensis Gupta and Verma in Gupta and Nakhasi, 1977a from Bos indicus and Bubalus bubalis in India; P. togolense Albaret, Bayssade-Dufour, Guilhon, Kulo and Picot, 1978 from sheep (experimental) in Togo and P. procapri Wang, 1979 and P. pseudo-cuonum Wang, 1979 from Procapra picticaudata and Canis familiaris respectively in China.

As shown above, the genus is in a state of confusion. The validity and generic positions of some species have been doubted. Even some species recently reported are insufficiently described. In view of this, it was felt that there is a need for re-examining critically as many species as possible. As a result, the genus Paramphistomum Fischoeder, 1901 is redefined and restricted. Eight species are retained and redescribed under the genus. An additional new species from Cephalophus nigrifrons in Rwanda is described and illustrated.

SYNONYMS: Liorchis Velichko, 1966

Srivastavaia Singh, 1970

GENERIC DIAGNOSIS

Paramphistomidae, Paramphistominae. Body conical, almost round in cross section; ventral pouch absent. Acetabulum subterminal, not enormous but moderate in size. Pharynx without pouch or diverticle; oesophagus without bulb or posterior sphincter; caeca in lateral sides of the body, sinuous or almost straight. Testes rounded or lobate, tandem or slightly diagonal; seminal vesicle thin-walled and coiled; pars musculosa short and weakly developed; pars prostatica moderately developed; cirrus pouch absent. Ovary and Mehlis' gland posttesticular; uterus winds forward, dorsal to the testes then ventral to the male ducts; Laurer's canal crosses the excretory vesicle or duct; vitellaria in lateral fields, may or may not be confluent dorso-medially. Genital sucker absent. Parasitic in the stomach of ruminants.

Type species: Paramphistomum cervi (Zeder, 1790) Fischoeder, 1901

Paramphistomum cervi (Zeder, 1790) Fischoeder, 1901

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos taurus	Königsberg (now Kaliningrad)	Naturhistoriska riksmuseet (Stockholm) coll. no. 397. Näsmark's material probably from the original materials of Fischoeder.
	Czechoslovakia	Dr. J. Pacenovský
	Germany	Prof. Dr. K. Odening
	Turkey	Prof. Dr. Fakhri Sayin
Cattle	Denmark	Dr. Aa. Henriksen
	England	Commonwealth Institute of Helminthology coll. no. 965.
	Ireland	British Museum (Natural History) coll. nos. 1951 12.11.51-60; 17/6/48.
		London School of Hygiene & Tropical Medicine coll. no. 4453.
	Netherlands	Dr. J. Jansen
Bos grunniens	Tibet	British Museum (Natural History) coll. no. 1965. 3.15.51-30.
		Institut für Parasitologie und Allgemeine Zoologie der Veterinärmedizinischen Universität (Vienna) coll. no. I/B259, presented by Dr. H. Prosl.

Capreolus sp.	Germany	Prof. Dr. K. Odening London School of Hygiene & Tropical Medicine, LeRoux collection.
Cervus elaphus	Austria	Institut für Parasitologie und Allgemeine Zoologie der Veterinärmedizinischen Universität (Vienna) coll. no. I/B258, presented by Dr. H. Prosl.
	Czechoslovakia	Dr. J. Pačenovský
Ovis sp.	Czechoslovakia	Dr. J. Pačenovský

HABITAT: Rumen and reticulum

DESCRIPTION:

Body conical, slightly bends ventrally, 5.50-13.23 mm long, 1.88-3.05 mm wide measured in the dorso-ventral direction at level of testes or acetabulum; body surface lacks tegumental papillae.

Acetabulum subterminal, external diameter 1.00-2.80 mm in the dorso-ventral direction; ratio to body length 1:4 to 1:5.6; of the paramphistomum type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 13-17; d.e.c.2, 22-33; d.i.c., 40-48; v.e.c., 17-21; v.i.c., 40-52; m.e.c., 6-9.

Pharynx 0.62-1.38 mm long; 0.44-0.88 mm wide measured in the dorso-ventral direction; ratio to body length 1:6.6 to 1:10.3, to the diameter of the acetabulum 1:1.1 to 1:2.4; of the liorchis type (sensu Näsmark, 1937) in median sagittal section; anterior half of internal surface lined by long papillae. Oesophagus 0.65-1.02 mm long, almost straight or may bend dorsally; musculature of wall relatively thin, no bulb or posterior sphincter; lumen lined by hyaline

layer throughout its length. Caeca lateral, almost straight in their course, reach anterior level of acetabulum and the blind ends are situated more in the dorsal side than in the lateral sides of the body.

Testes lobed, tandem in middle of the body, preovarian; anterior testis 0.66-1.84 mm long, 1.29-1.88 mm in the dorso-ventral direction. Seminal vesicle long, strongly coiled and thin-walled; pars musculosa very short and weakly developed; pars prostatica 0.17-0.44 mm long and 0.16-0.33 mm wide.

Ovary subspherical, unlobed, posttesticular and preacetabular, 0.38-0.83 by 0.31-0.67 mm. Mehlis' gland close to ovary, 0.21-0.56 by 0.18-0.50 mm; Laurer's canal crosses excretory vesicle or duct, opens on dorsal surface about 0.15-1.11 mm posteriorly to the excretory pore; uterine coils dorsal to testes and ventral to the male ducts; vitellaria follicular, in lateral sides of the body from level of pharynx to acetabulum, not confluent medially in their posterior or anterior limits; egg 123-160 by 65-96 µm.

Genital pore bifurcal or immediately postbifurcal; terminal genitalium of the gracile type (sensu Näsmark, 1937) with well developed genital papilla.

Excretory vesicle antero-dorsal to acetabulum; excretory pore anterior to Laurer's canal opening at level of posterior testis.

FIGURE 37

Paramphistomum cervi (Zeder, 1790) Fischoeder, 1901

(SEM)

a. Whole worm, ventral view (scale bar = 500 µm)

b. Genital pore region with genital papilla everted, lateral view (scale bar = 100 µm)

c. Anterior end (scale bar = 200 µm)

d. Genital pore region, front view (scale bar = 200 µm)

e. Acetabular region (scale bar = 200 µm)

Note the absence of papillae on the surfaces.

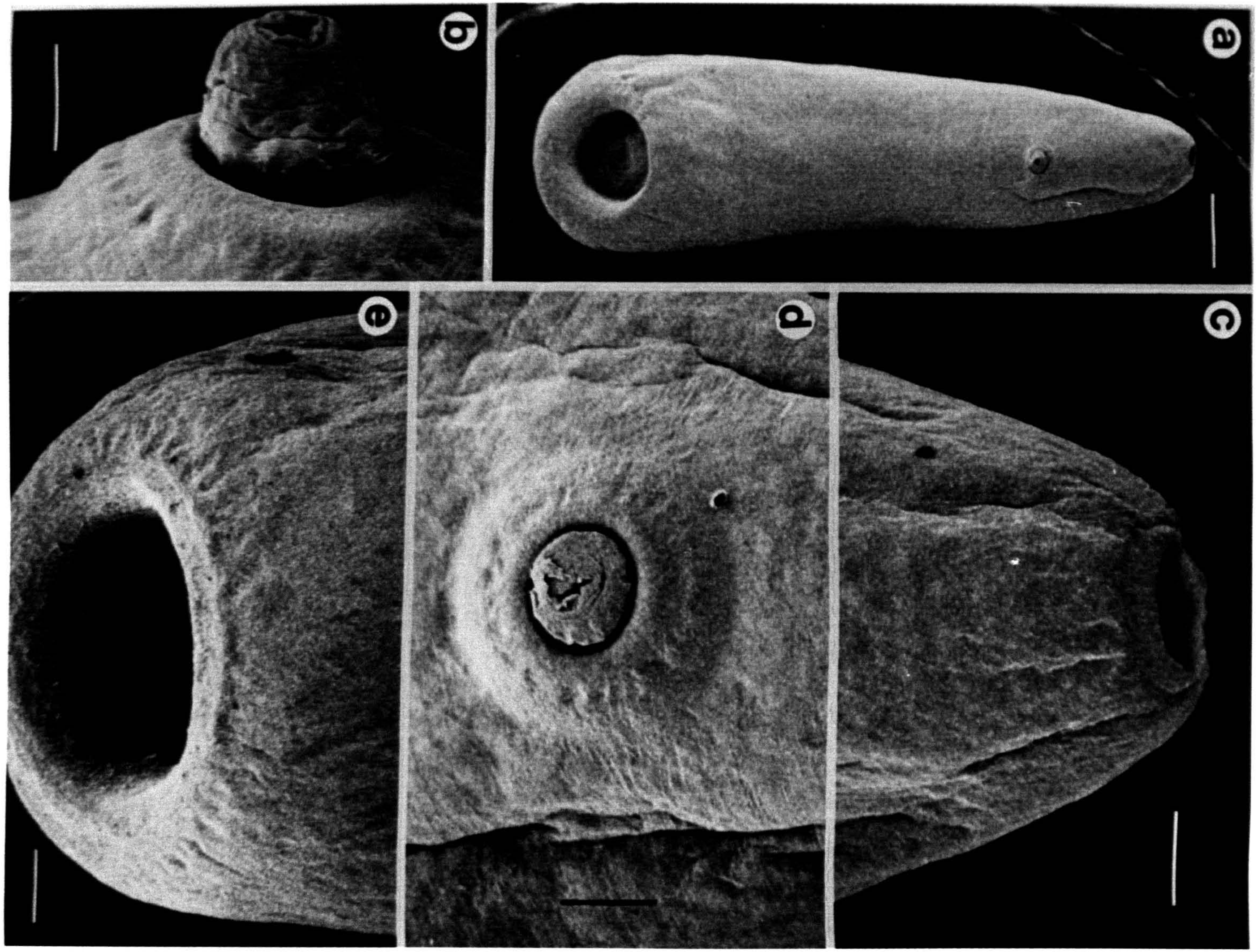

a
b
c
d
e

FIGURE 38

Paramphistomum cervi (Zeder, 1790) Fischoeder, 1901

a. Whole worm, ventral view

b. Whole worm, sagittal view

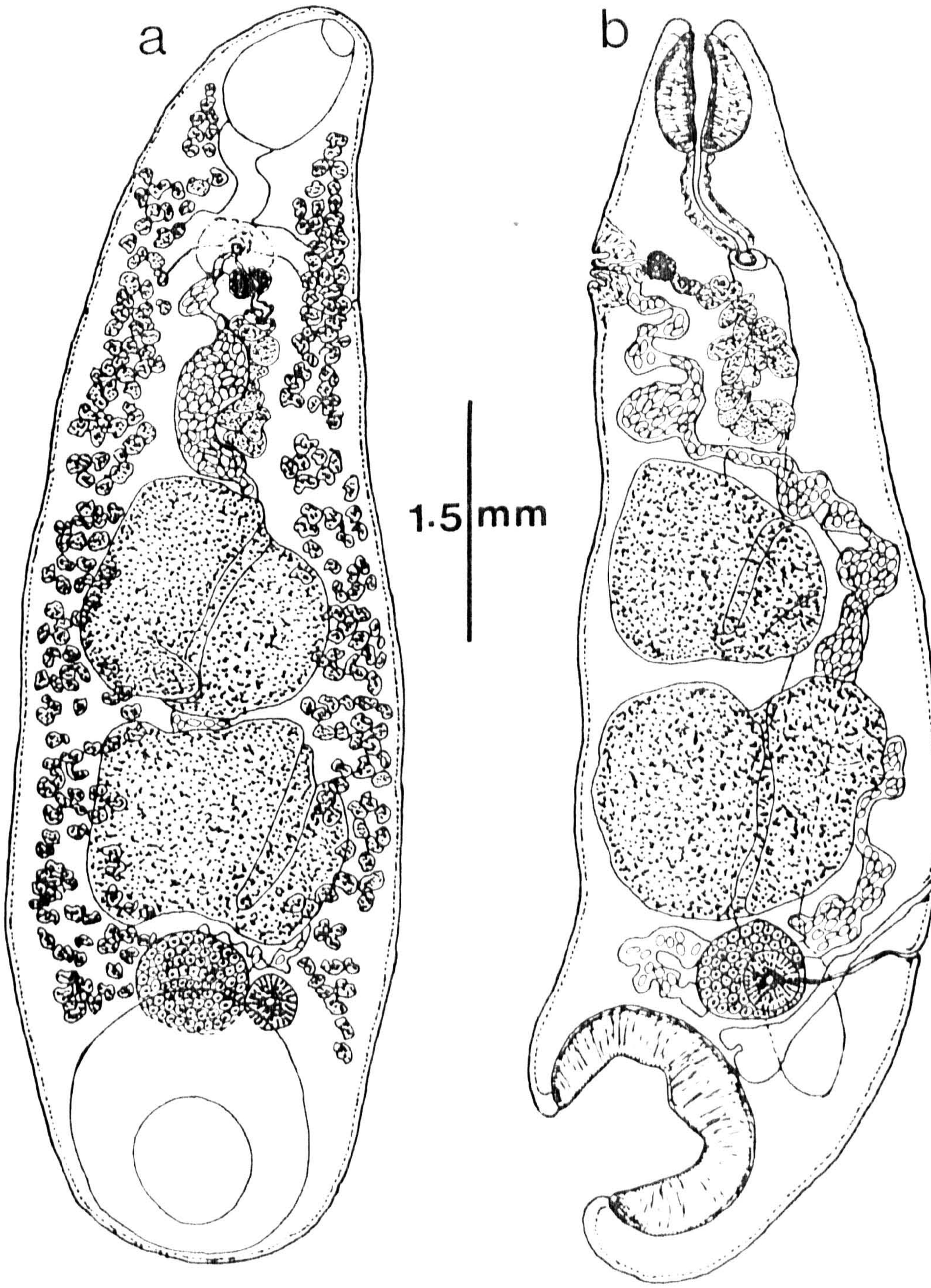

a
b
1.5 mm

FIGURE 39

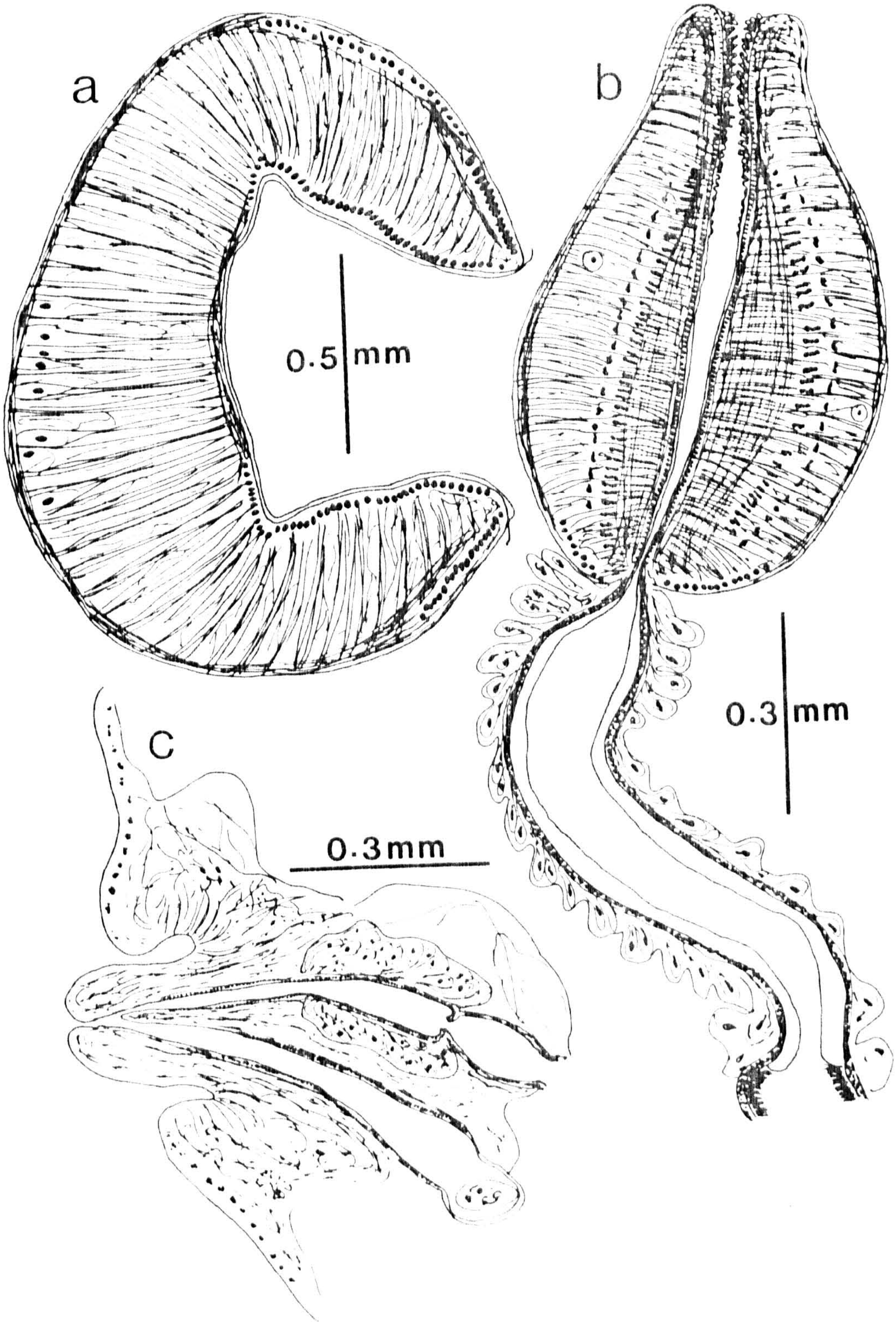
Paramphistomum cervi (Zeder, 1790) Fischoeder, 1901

(median sagittal section)

a. Acetabulum (paramphistomum type)

b. Pharynx (liorchis type) and oesophagus

c. Terminal genitalium (gracile type)


a
0.5 mm
b
0.3 mm
C
0.3mm

Paramphistomum gracile Fischoeder, 1901

Synonyms: Paramphistomum indicum Stiles and Goldberger, 1910 in part

Paramphistomum bombayiensis Gupta and Verma in Gupta and Nakhasi, 1977a

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities, donors/collections

Bos indicus	Sri Lanka	Naturhistoriska riksmuseet (Stockholm) coll. no. M1-5. Näsmark's material from the original materials of Fischoeder.
Bubalus bubalis	Sri Lanka	Naturhistoriska riksmuseet (Stockholm) coll. nos. 2946, 2947, 2956, 1952, Näsmark's material.
Ovis sp.	Bangkok, Thailand	Commonwealth Institute of Helminthology coll. no. 2334.

HABITAT: Rumen

DESCRIPTION:

Body conical, slender, nearly straight, 5.95-11.2 mm long, 1.76-3.00 mm in greatest width measured in the dorso-ventral direction; body surface has short and stumpy papillae covered with hair-like processess and these are present only on the anterior end around the oral opening.

Acetabulum subterminal, 1.38-1.83 mm in external diameter in the dorso-ventral direction; ratio to body length 1:4.8 to 1:7.1; of the paramphistomum type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 15-22; d.e.c.2, 28-40; d.i.c., 34-46; v.e.c., 15-21; v.i.c., 42-57; m.e.c., 7-24.

Pharynx 0.61-1.19 mm long, 0.35-0.76 mm in the dorso-ventral direction; ratio to body length 1:7.8 to 1:9.7, to the diameter of the acetabulum 1:1.3 to 1:2.3; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section; internal surface lined by small dome-shaped papillae. Oesophagus 0.55-1.41 mm long, almost straight; musculature of wall relatively thin, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form irregular dorso-ventral bends, may or may not reach level of acetabulum, blind ends directed posteriorly.

Testes deeply lobed, tandem in posterior half of the body; anterior testis 0.81-1.11 mm long, 0.77-0.99 mm in the dorso-ventral direction; posterior testis 0.59-1.31 mm long, 0.54-1.27 mm in the dorso-ventral direction; seminal vesicle long, strongly coiled and thin-walled; pars musculosa short and weakly developed; pars prostatica 0.23-0.46 by 0.23-0.26 mm in size.

Ovary round to subspherical, situated between testis and acetabulum in the posterior part of the body, 0.34-0.45 by 0.31-0.39 mm. Mehlis' gland close to or immediately posterior to ovary, 0.15-0.36 by 0.26-0.32 mm; Laurer's canal crosses excretory vesicle or duct, opens on the dorsal surface about 0.55-1.15 mm posteriorly to the excretory pore. Uterine coils dorsal to testes then ventral to the male ducts; vitellaria in lateral fields, sparsely scattered from level of oesophagus to the anterior border of the acetabulum, not confluent medially in their anterior and posterior limits; egg 120-124 by 69-70 µm.

Genital pore distinctly at the level posterior to the oesophageal bifurcation (about 0.45-0.70 mm posterior to it); terminal genitalium of the gracile type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at the level of the posterior testis or between the two testes and anteriorly to the Laurer's canal opening.

FIGURE 40

Paramphistomum gracile Fischoeder, 1901

(SEM)

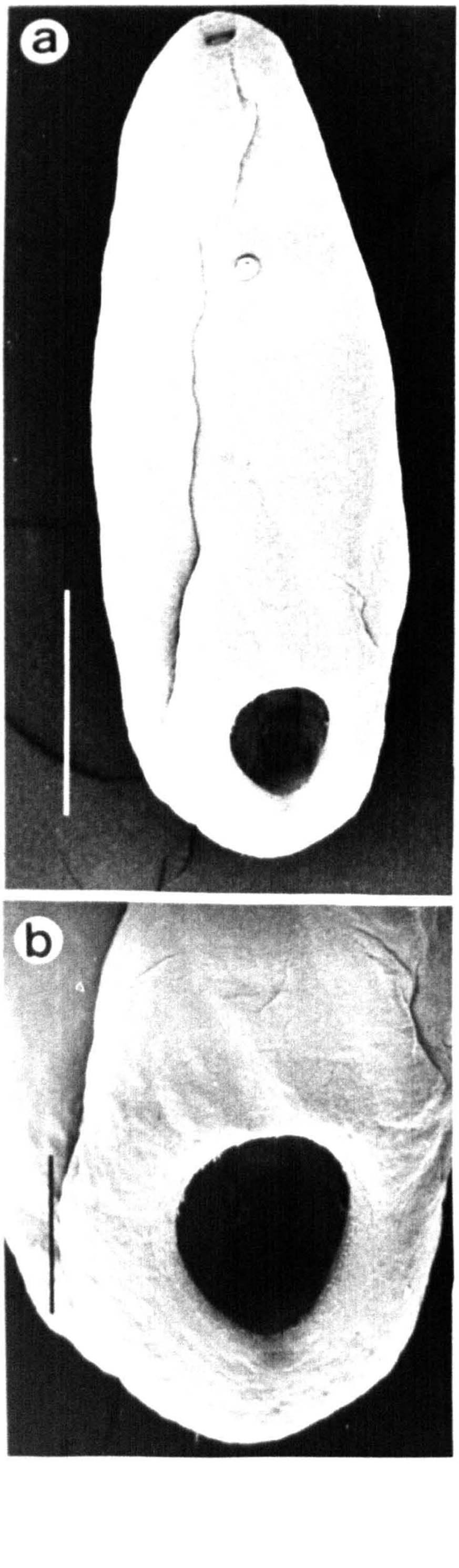
a. Whole worm, ventral view (scale bar = 1 mm)

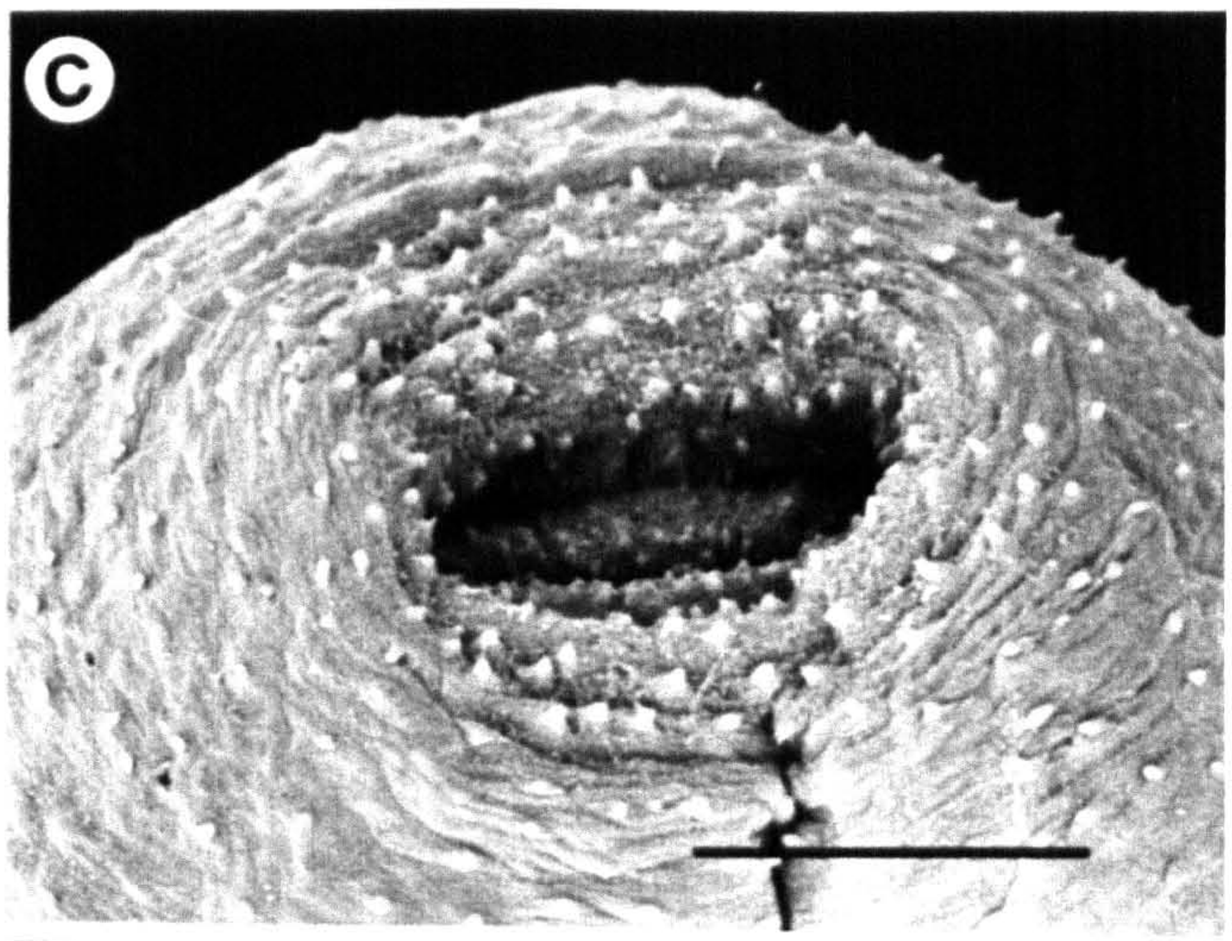
b. Acetabular region (scale bar = 500 µm)

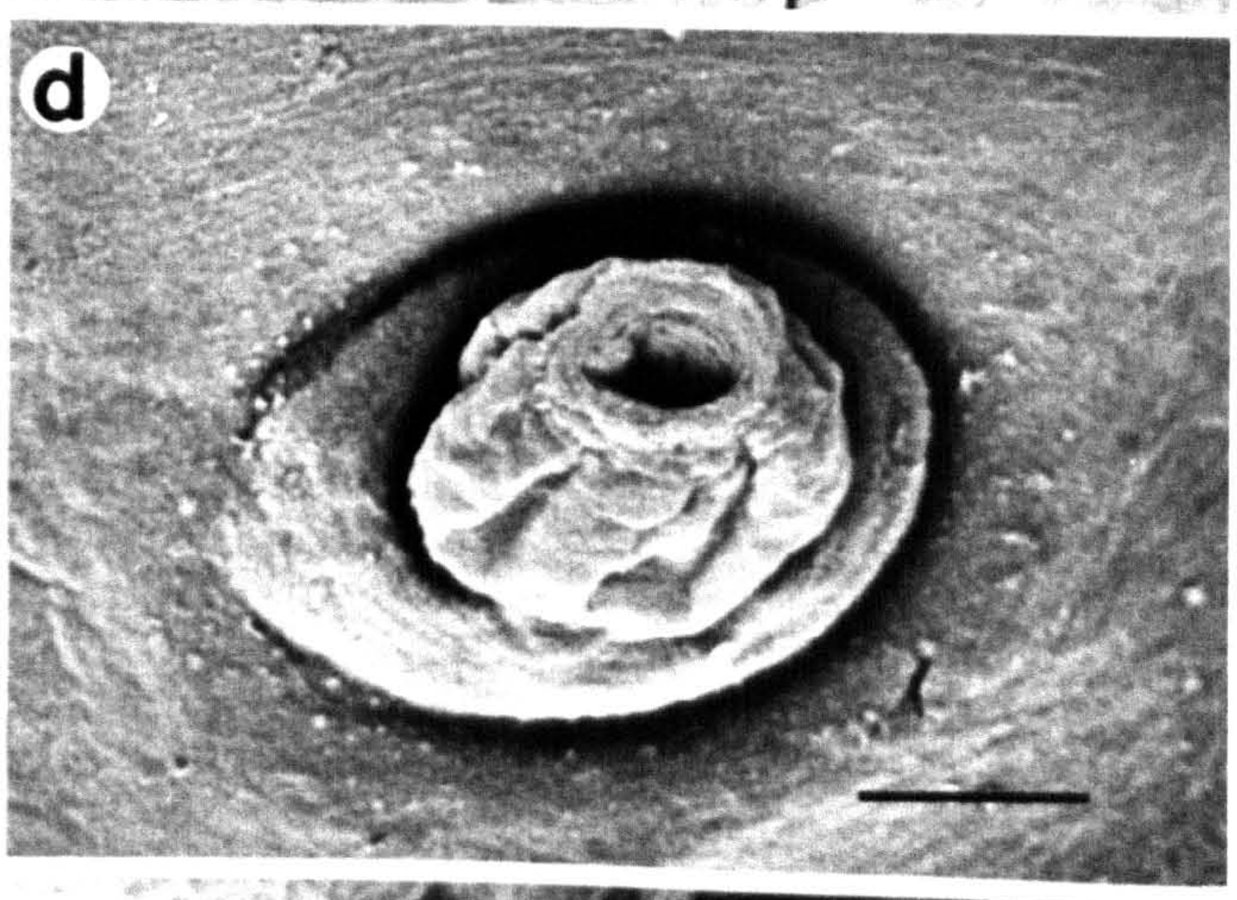
c. Anterior end, note presence of tegumental papillae (scale bar = 150 µm)

d. Genital pore region with genital papilla everted (scale bar = 50 µm)

e. Closer view of papillae on anterior end, note stumpy form and covered with hair-like processess (scale bar = 3 µm)


a


c


d

b

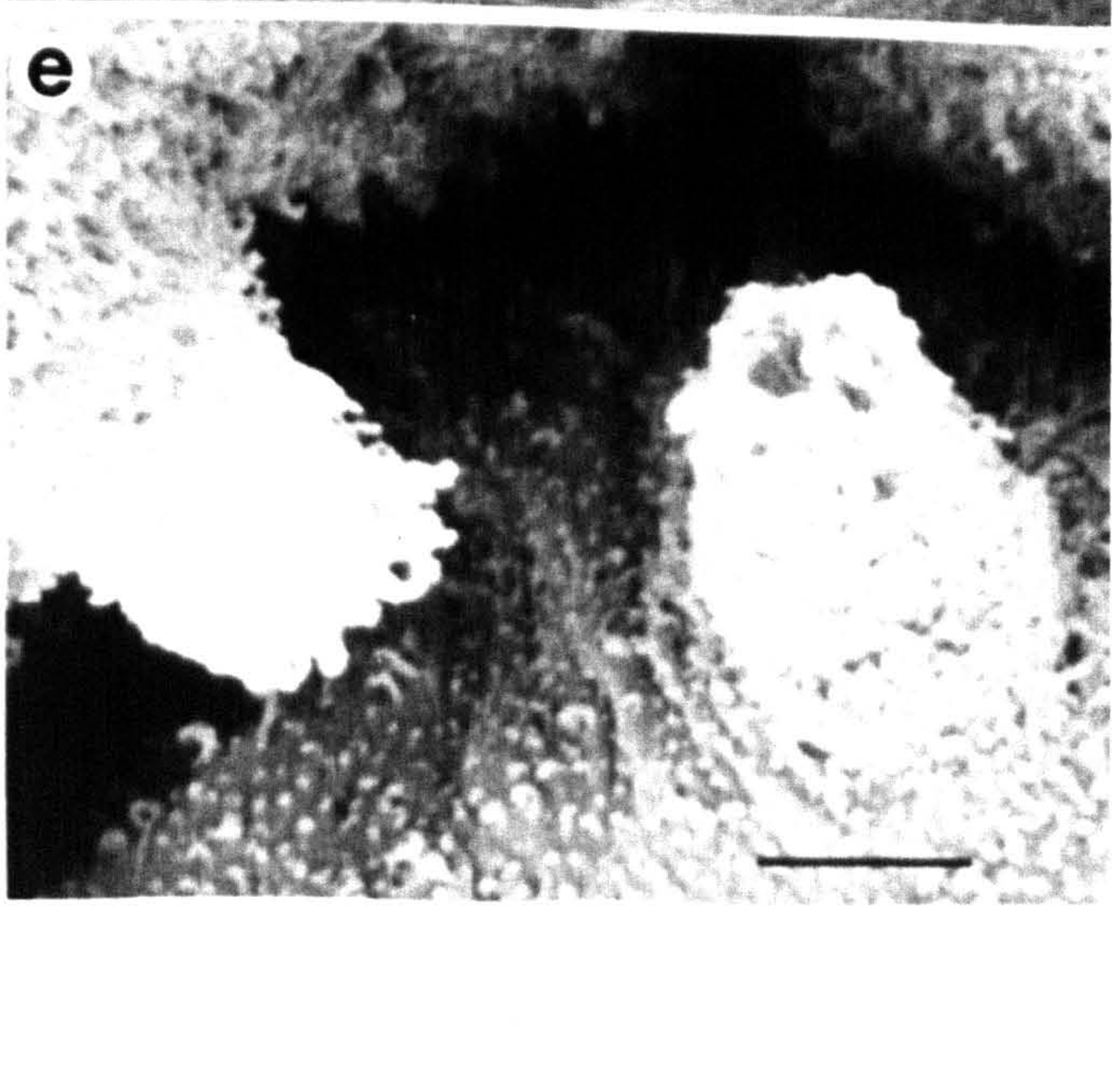

e

FIGURE 41

Paramphistomum gracile Fischoeder, 1901

a. Whole worm, ventral view

b. Whole worm, sagittal view

a

b

2 mm

FIGURE 42

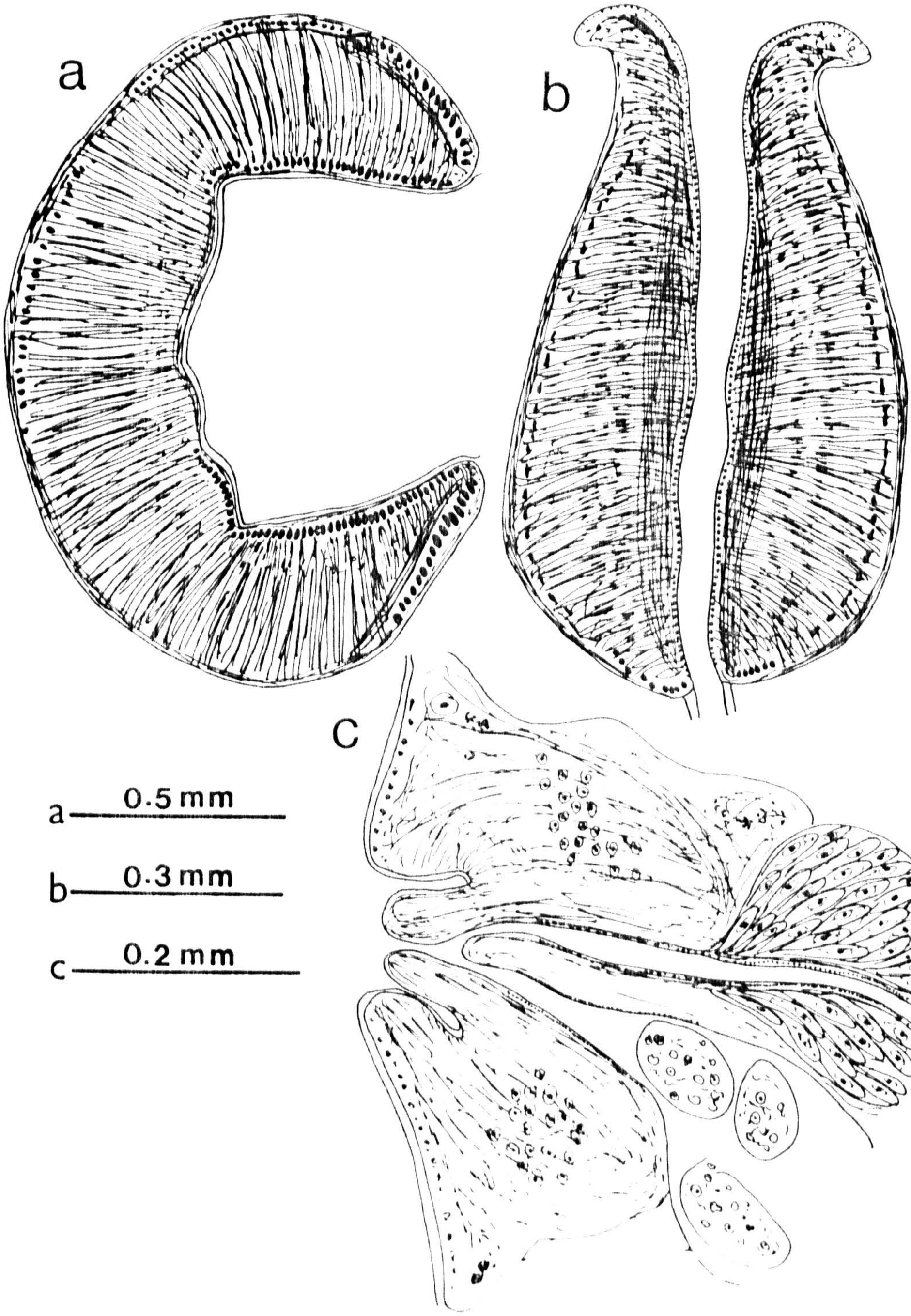
Paramphistomum gracile Fischoeder, 1901

(median sagittal section)

a. Acetabulum (paramphistomum type)

b. Pharynx (calicophoron type)

c. Terminal genitalium (gracile type) and part of pars prostatica and uterus.


a
b
C
a 0.5 mm
b 0.3 mm
c 0.2 mm

Paramphistomum liorchis Fischoeder, 1901

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collections

Mazama americana	Mato Grosso, Brazil	Instituto Oswaldo Cruz (Rio de Janeiro) coll. no. 11085, presented by Dr. Delir Correa Gomez.
Mazama namby	Brazil	London School of Hygiene & Tropical Medicine coll. no. 2061.
Mazama simplicicornis	Brazil	Naturhistoriska riksmuseet (Stockholm) coll. no. 395, Nasmark's material.
	?	London School of Hygiene & Tropical Medicine coll. no. 2071.

HABITAT: Rumen

DESCRIPTION:

Body conical, almost straight or may bend slightly ventrally, 3.12-9.23 mm long, 0.71-1.98 mm in greatest width measured in the dorso-ventral direction; body surface has small dome-shaped papillae concentrated around the oral opening and ventrally from this area to the middle of the body.

Acetabulum subterminal, external diameter 0.95-1.72 mm in the dorso-ventral direction; ratio to body length 1:3.8 to 1:5.3; of the paramphistomum type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 10-15; d.e.c.2, 20-28; d.i.c., 23-39; v.e.c., 12-16; v.i.c., 38-45; m.e.c., 10-20.

Pharynx 0.57-1.02 mm long, 0.29-0.55 mm wide in the dorso-ventral direction; ratio to body length 1:6.3 to 1:7.4, to the diameter of the acetabulum 1:1.3 to 1:1.8; of the liorchis type (sensu Näsmark, 1937) in median sagittal section; anterior two third of internal surface lined by long papillae. Oesophagus 0.29-0.51 mm long; musculature of wall relatively thin, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form irregular shallow dorso-ventral bends or sometimes may be almost straight in their course, reach level of acetabulum posteriorly and blind ends directed posteriorly.

Testes lobed, tandem in posterior half of the body, closer to ventral wall than to dorsal wall; anterior testis 0.71-1.56 mm long, 0.61-1.50 mm in the dorso-ventral direction; posterior testis 0.53-1.27 mm long, 0.47-1.36 mm in the dorso-ventral direction. Seminal vesicle relatively long, strongly coiled and thin walled; pars musculosa short and weakly developed; pars prostatica relatively small, almost as long as it is wide (0.19-0.21 by 0.26-0.30 mm in size).

Ovary subspherical, posttesticular and dorsal to acetabulum, 0.21-0.39 by 0.11-0.28 mm; Mehlis' gland close to or immediately posterior to ovary, 0.19-0.25 by 0.20-0.24 mm; Laurer's canal crosses excretory vesicle or duct, opens on the dorsal surface about 0.29-0.36 mm posteriorly to the excretory pore. Uterine coils dorsal to testes and ventral to the male ducts; vitellaria in lateral fields of the body, extend from level of pharynx to acetabulum, not confluent medially in their anterior and posterior limits. Egg 126-135 by 63-69 µm.

Genital pore at level of pharynx or oesophagus; terminal genitalium of the liorchis type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at the level between ovary and posterior testis.

FIGURE 43

Paramphistomum liorchis Fischoeder, 1901

(SEM)

a. Whole worm, ventral view. Note tegumental papillae on anterior half (scale bar = 200 µm)

b. Anterior end, note dome-shaped papillae (scale bar = 100 µm)

c. Genital pore region (scale bar = 50 µm)

d. Acetabular region (scale bar = 100 µm)

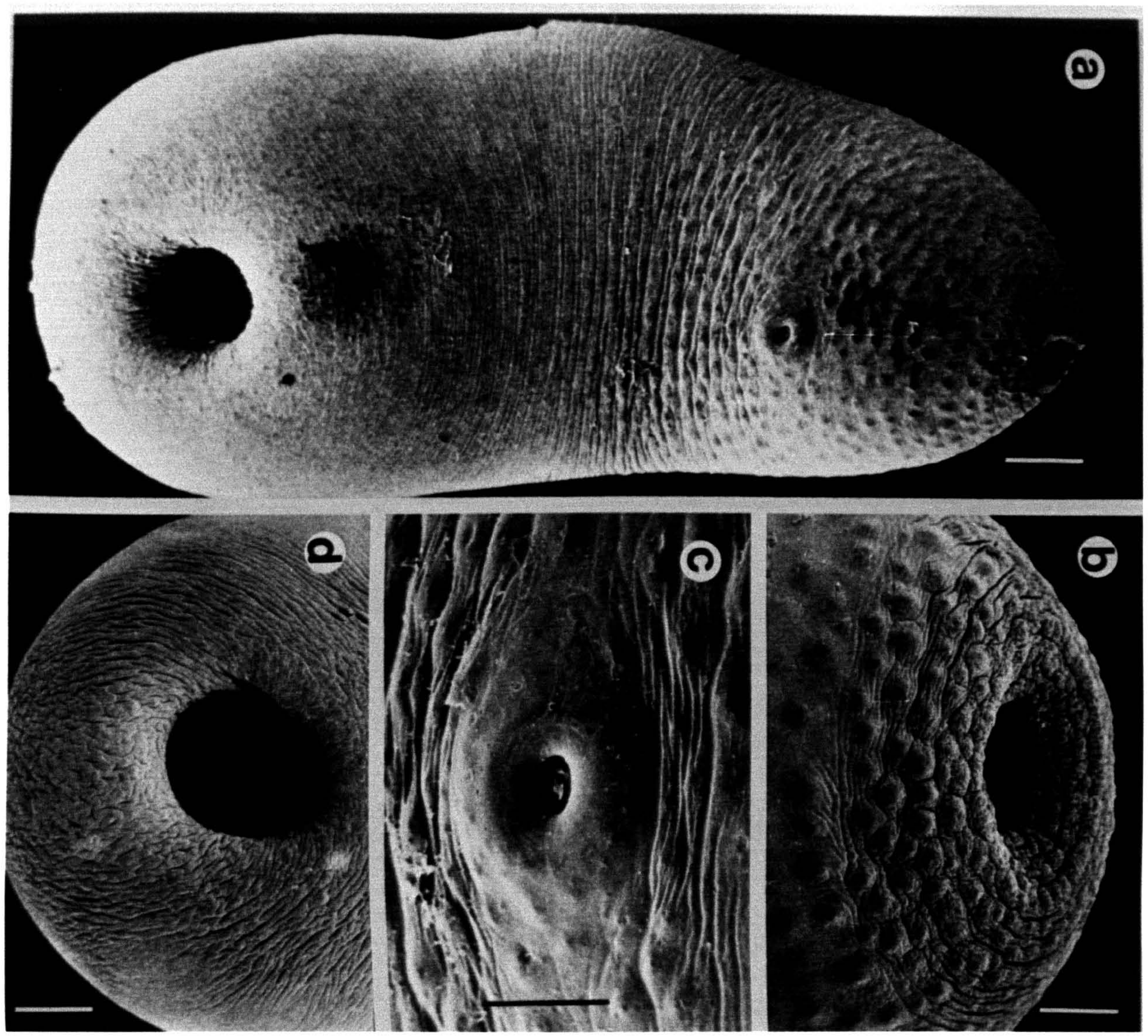

a
d
c
b

FIGURE 44

Paramphistomum liorchis Fischoeder, 1901

a. Whole worm, ventral view

b. Whole worm, sagittal view

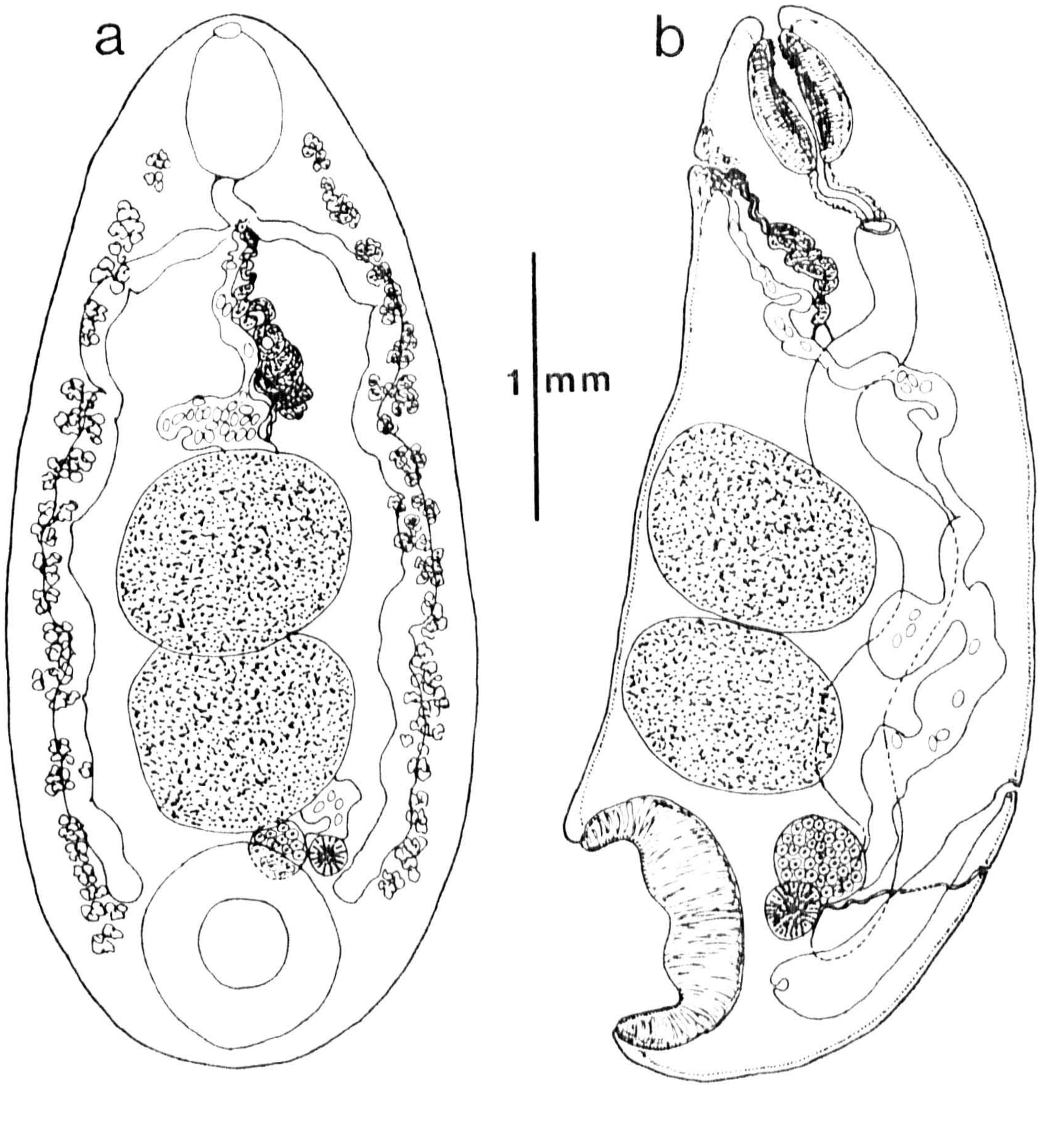

a
b
1 mm

FIGURE 45

Paramphistomum liorchis Fischoeder, 1901

(median sagittal section)

a. Acetabulum (paramphistomum type)

b. Pharynx (liorchis type)

c. Terminal genitalium (liorchis type) and pars prostatica

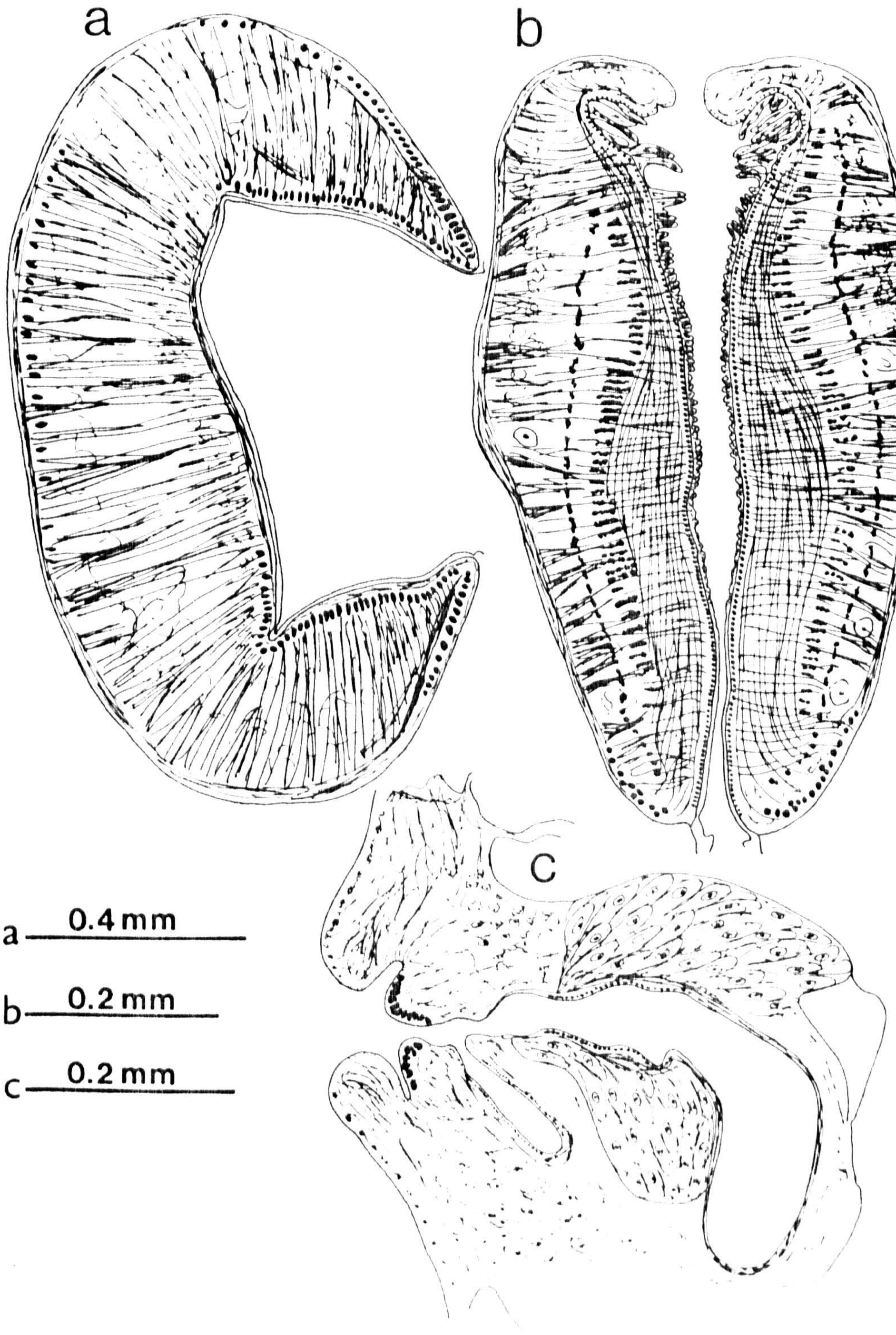

a
b
C
a 0.4mm
b 0.2mm
c 0.2mm

FIGURE 46

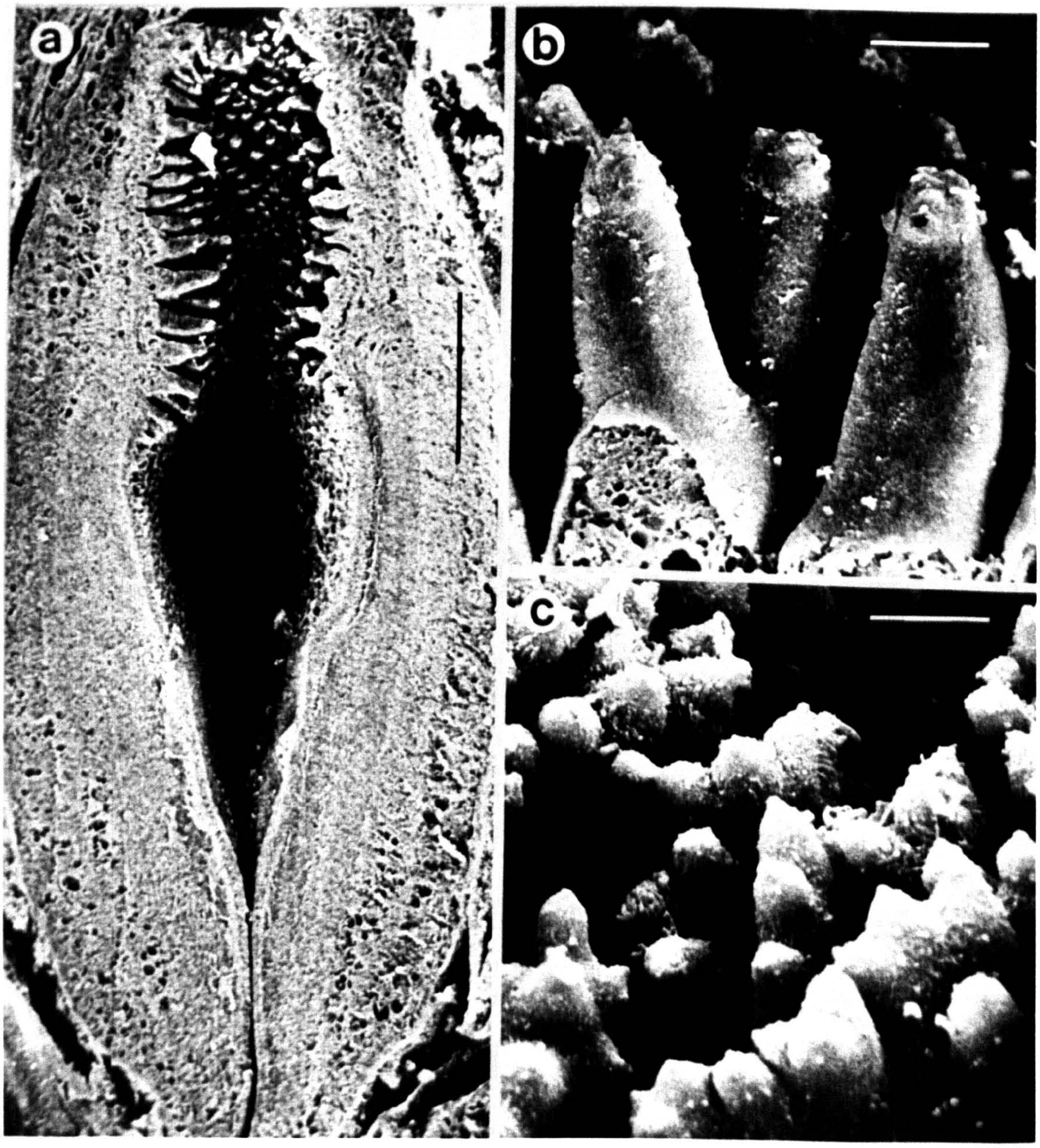
Paramphistomum liorchis Fischoeder, 1901

Internal surface of pharynx (SEM)

a. General view, note papilla on anterior two third of the surface (scale bar = 100 µm)

b. Closer view of papillae on anterior one third of the surface (scale bar = 10 µm)

c. Closer view of papillae on middle third of the surface (scale bar = 10 µm)


a
b
c

Paramphistomum epiclitum Fischoeder, 1904

Synonyms: Paramphistomum indicum Stiles and Goldberger, 1910 in part
Paramphistomum thapari Price and McIntosh, 1953
Paramphistomum malayi Lee and Lowe, 1971
Cotylophoron indicum Stiles and Goldberger, 1910
Cotylophoron madrasense Gupta, 1958
Cotylophoron chauhani Gupta and Gupta, 1972
Srivastavaia indica Singh, 1970

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos indicus	Rangoon, Burma	British Museum (Natural History) coll. no. 1957. 12.30.225.265 labeled "P. cauliorchis".
Cattle	Dacca, Bangladesh	British Museum (Natural History) coll. no. 1968. 2.27.31-50.
	India	London School of Hygiene & Tropical Medicine coll. nos. 580, 635, 1818.
Bubalus bubalis	India	Naturhistoriska riksmuseet (Stockholm) coll. nos. AC1-2, N1-3, Näsmark's material.
		London School of Hygiene & Tropical Medicine coll. nos, 703, 818.
		Commonwealth Institute of Helminthology, Dr. J.A. Dinnik's collection labeled "Srivastavaia indica".

Capra hircus	Burma	British Museum (Natural History) coll. no. 1957.12.30.225-265.
Goat	Rangoon, Burma	London School of Hygiene & Tropical Medicine coll. no. 5099.
	Assam, India	London School of Hygiene & Tropical Medicine coll. no. 4369.
	India	British Museum (Natural History) coll. no. 1967.3.15.1-200.
Sheep	India	London School of Hygiene & Tropical Medicine coll. no. 4494.
		British Museum (Natural History) coll. no. 1967.3.15.1-200.

HABITAT: Rumen

DESCRIPTION:

Body conical, bends ventrally. 5.30-9.10 mm long, 0.82-2.40 mm in greatest width in the dorso-ventral direction; body surface has dome shaped papillae concentrated around the oral opening and ventrally from this point to about the middle of the body or slightly beyond it and smaller papillae randomly arranged around the acetabular opening.

Acetabulum subterminal, external diameter 1.02-1.82 mm in the dorso-ventral direction, ratio to body length 1:3.5 to 1:4.9; of the paramphistomum type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 10-26; d.e.c.2, 30-43; d.i.c., 30-56; v.e.c., 11-23; v.i.c., 30-59; m.e.c., 21-28.

Pharynx 0.60-1.01 mm long, 0.31-0.77 mm in the dorso-ventral direction; ratio to body length 1:6.9 to 1:9.1, to the diameter of the acetabulum 1:1.6 to 1:2.5; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section, internal surface lined by small dome-shaped papillae. Oesophagus 0.40-1.09 mm long, may bend dorsally; musculature of wall of moderate thickness, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form fairly uniform dorso-ventral bends, blind ends reach level of acetabulum and directed ventrally.

Testes deeply lobed, tandem in posterior half of the body; anterior testis 0.51-1.10 mm long, 0.77-1.48 mm in the dorso-ventral direction. Seminal vesicle long, strongly coiled and thin-walled; pars musculosa short and weakly developed; pars prostatica large and well developed, nearly as long as it is wide (0.25-0.55 by 0.33-0.80 mm).

Ovary subspherical, posttesticular and dorsal to acetabulum, 0.24-0.40 by 0.30-0.39 mm; Mehlis' gland close to or immediately posterior to ovary, 0.23-0.31 by 0.20-0.34 mm; Laurer's canal crosses excretory vesicle or duct and opens on the dorsal surface about 0.76-1.06 mm posteriorly to the excretory pore; uterine coils dorsal to testes then ventral to the male ducts; vitellaria in lateral fields of the body, extend from level of oesophagus to acetabulum, not confluent medially in their anterior or posterior limits; egg 145-150 by 83-85 µm.

Genital pore consistently at a level posterior to the oesophageal bifurcation about 0.32-0.57 mm posteriorly to it; terminal genitalium of the epiclitum type (sensu Näsmark, 1937)

characterized by a wall which is semi-circular in outline giving a false impression of a sucker.

Excretory vesicle consists of two expanded chambers connected by a narrow isthmus; excretory pore opens on the dorsal surface at level of the anterior testis or between the two testes and anteriorly to the Laurer's canal opening.

FIGURE 47

Paramphistomum epiclitum Fischoeder, 1904

(SEM)

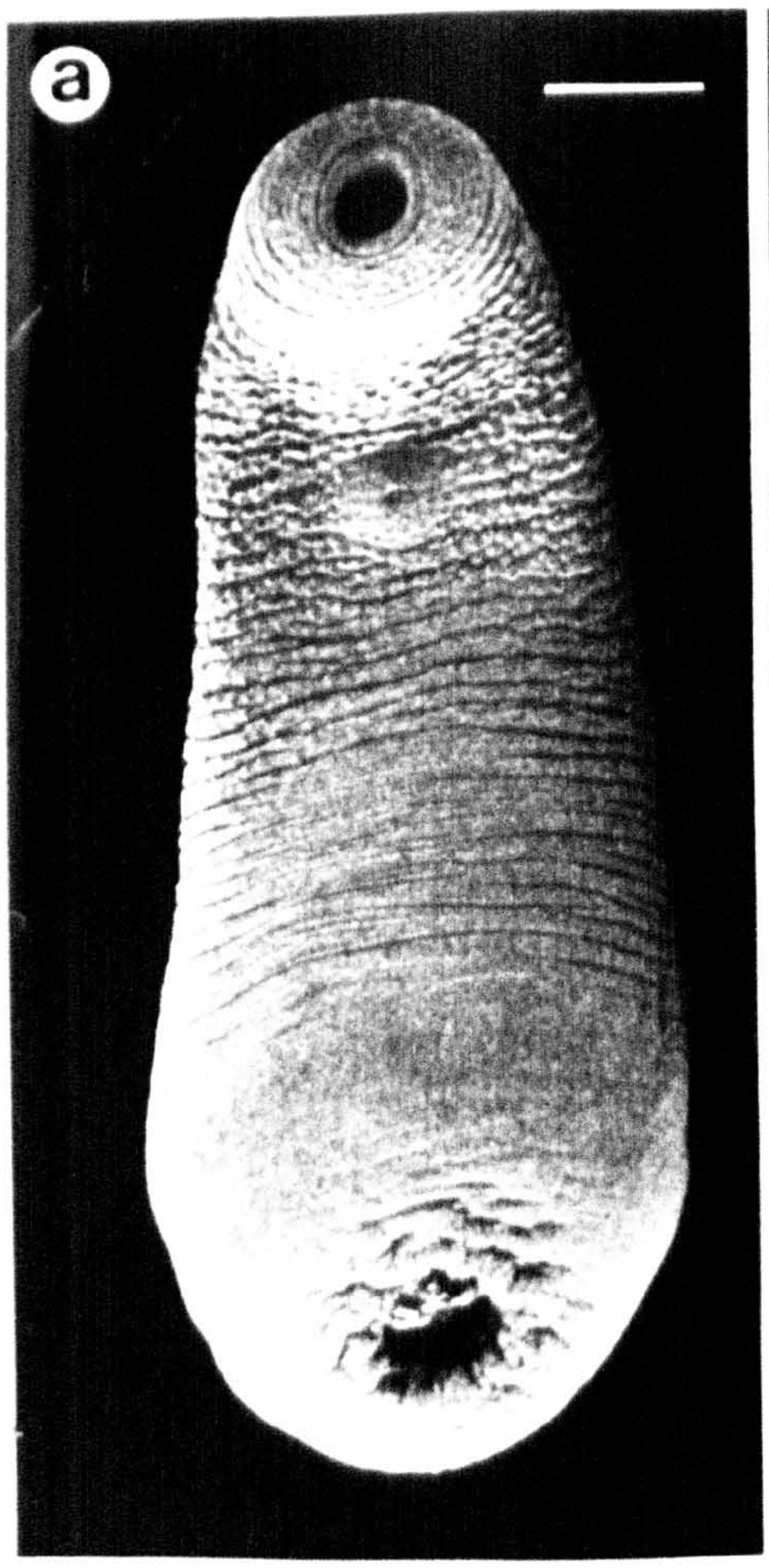
a. Whole worm, ventral view. Note large papillae on anterior half (scale bar = 500 µm)

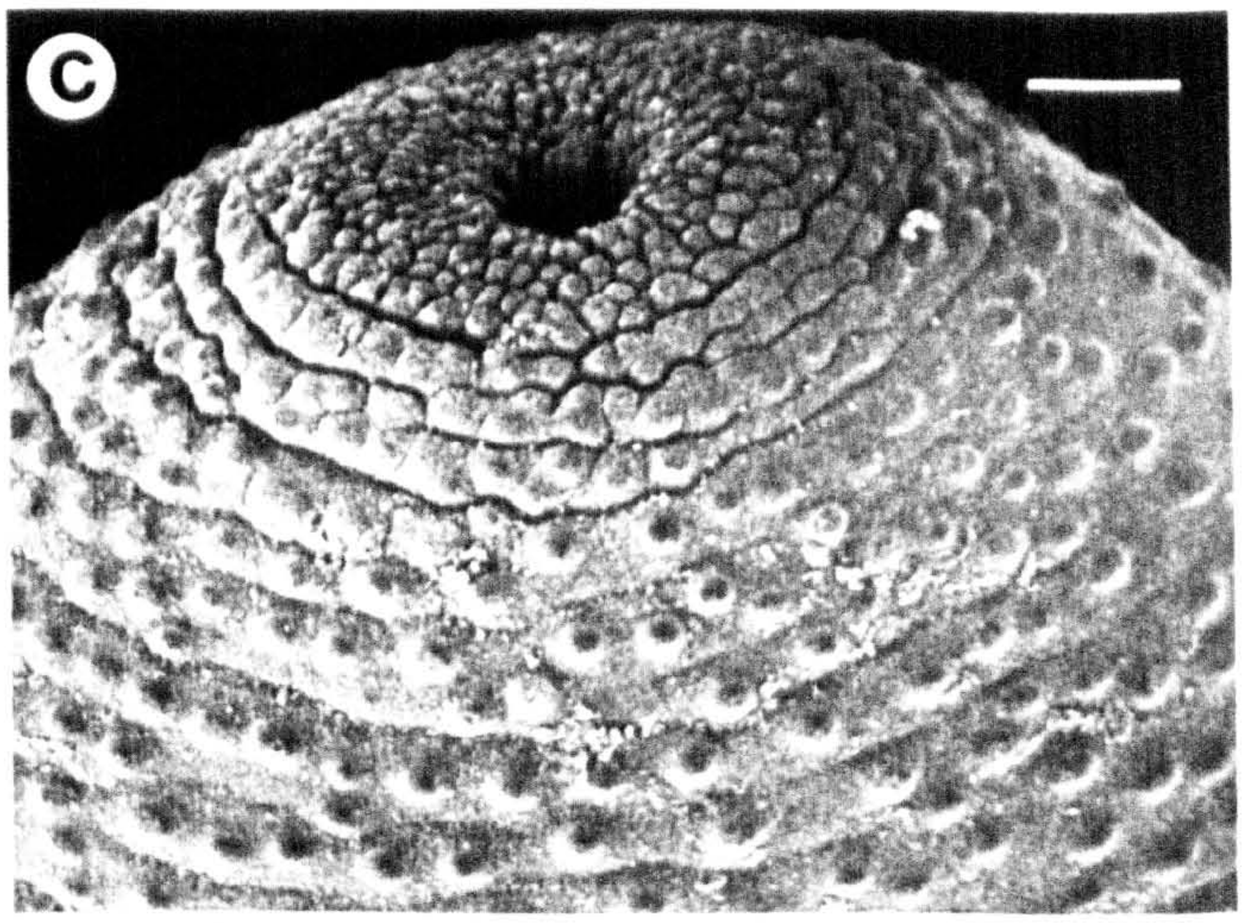
b. Closer view of tegumental papillae, dome-shaped and smooth (scale bar = 50 µm)

c. Anterior end (scale bar = 100 µm)

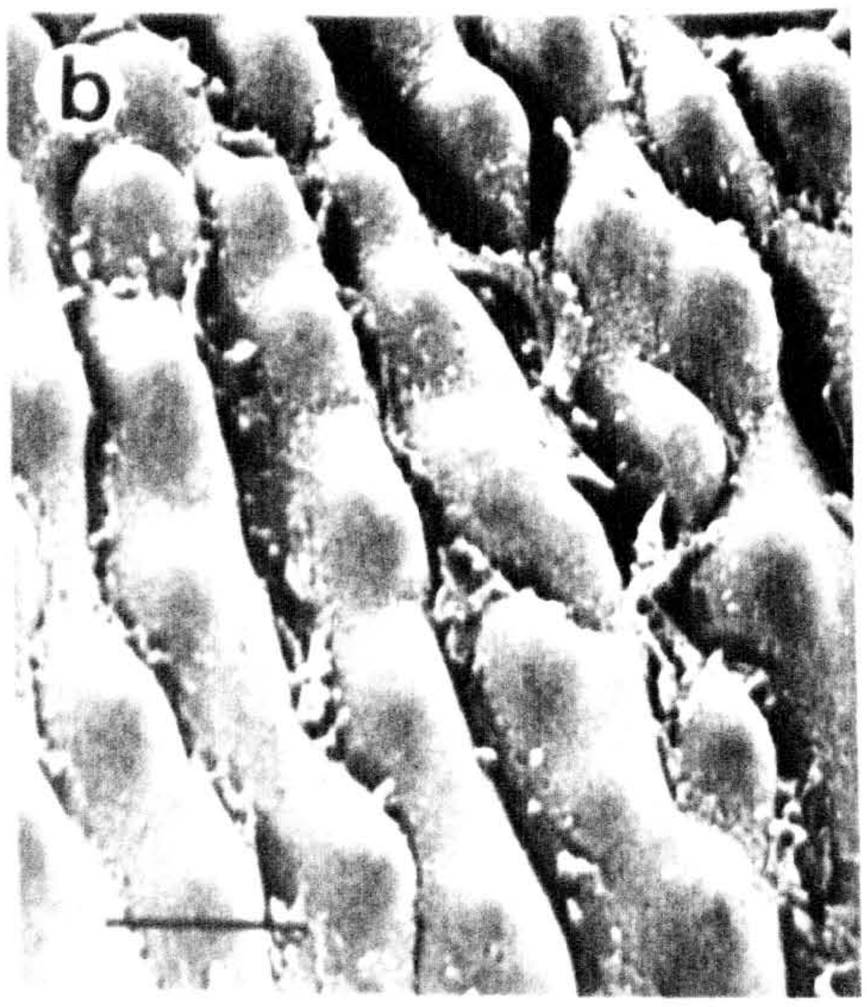
d. Genital pore region (scale bar = 100 µm)

e. Acetabular region, note much smaller and randomly arranged papillae (scale bar = 100 µm)


a


c


d


b

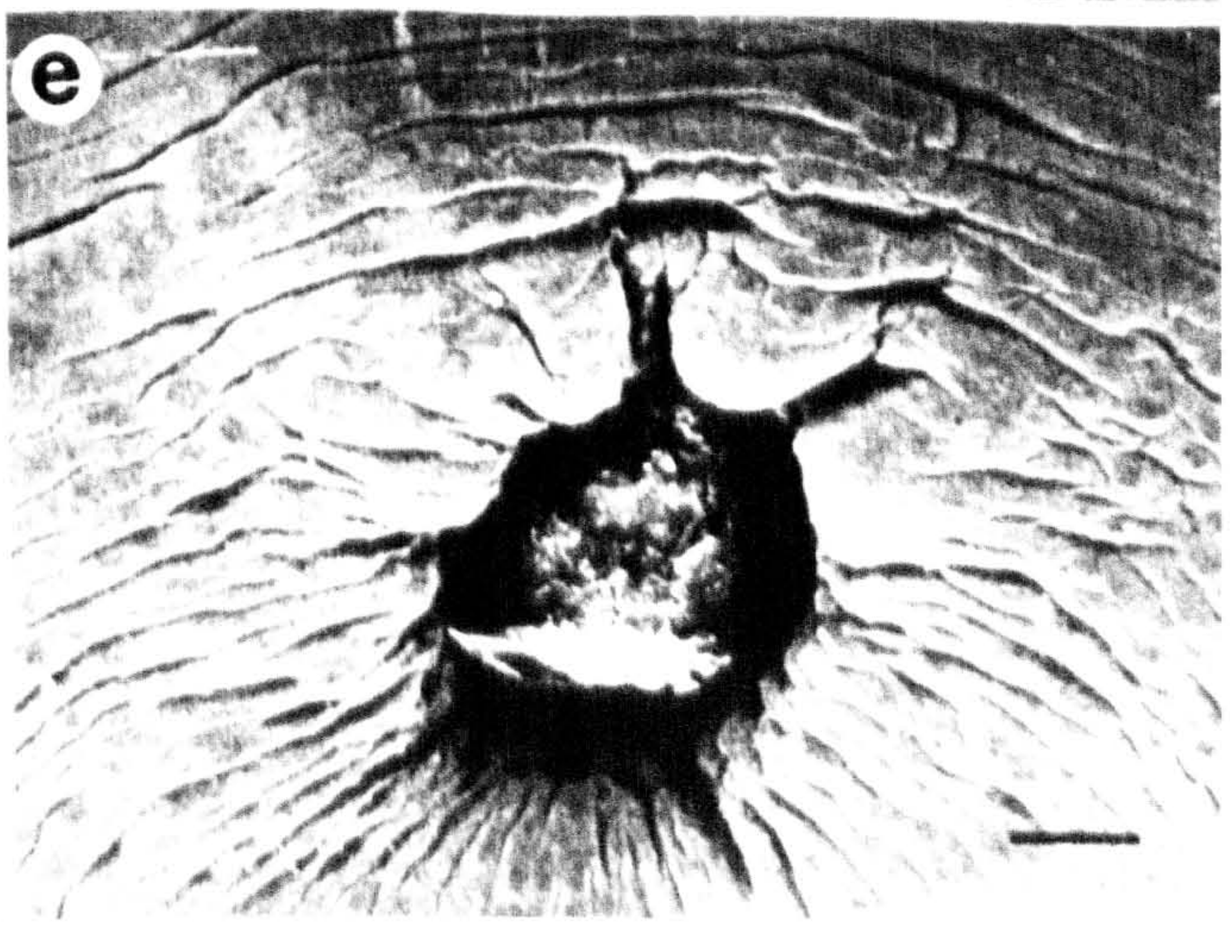

e

FIGURE 48

Paramphistomum epiclitum Fischoeder, 1904

a. Whole worm, ventral view

b. Whole worm, sagittal view

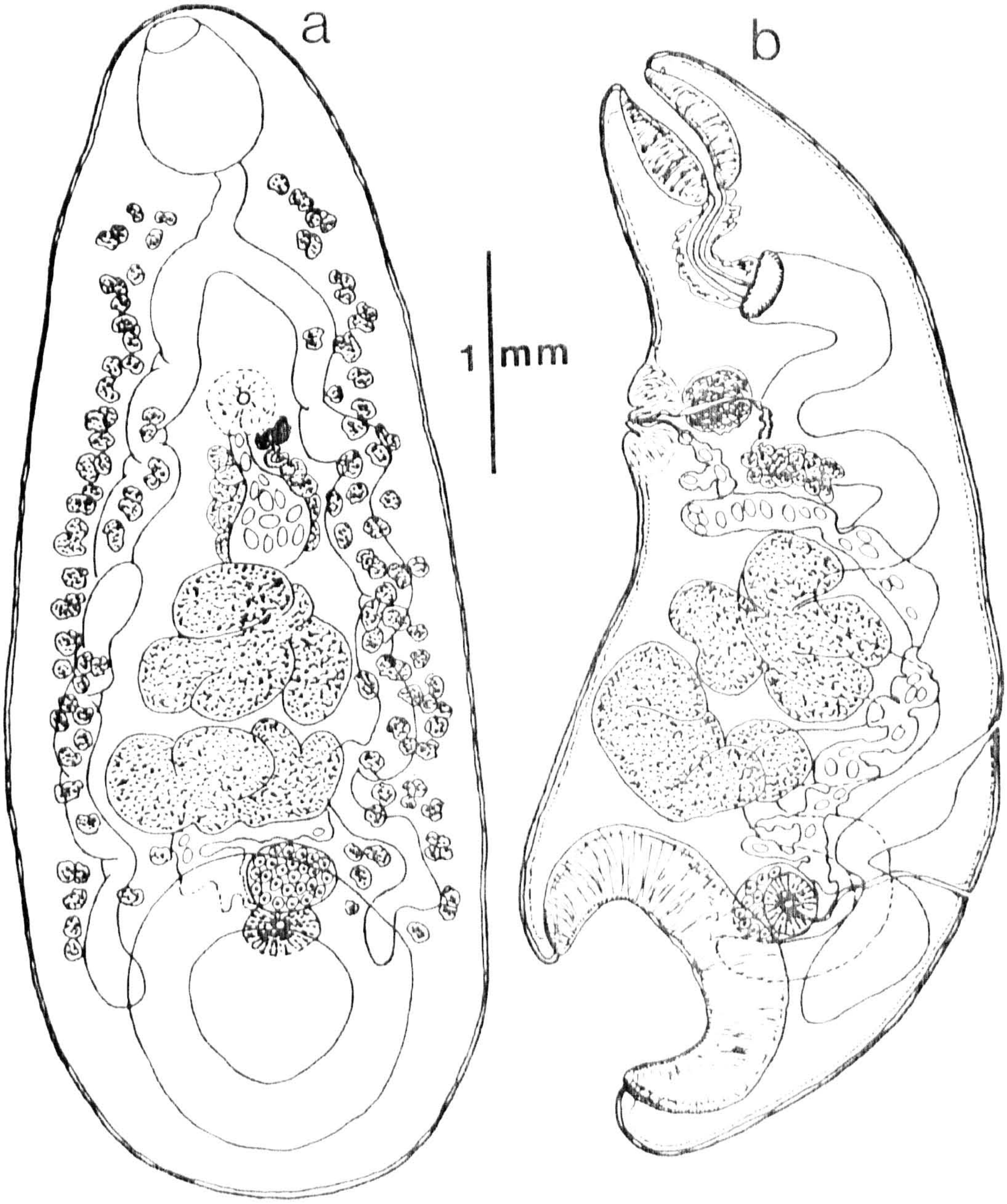

a
b
1 mm
b

FIGURE 49

Paramphistomum epiclitum Fischoeder, 1904

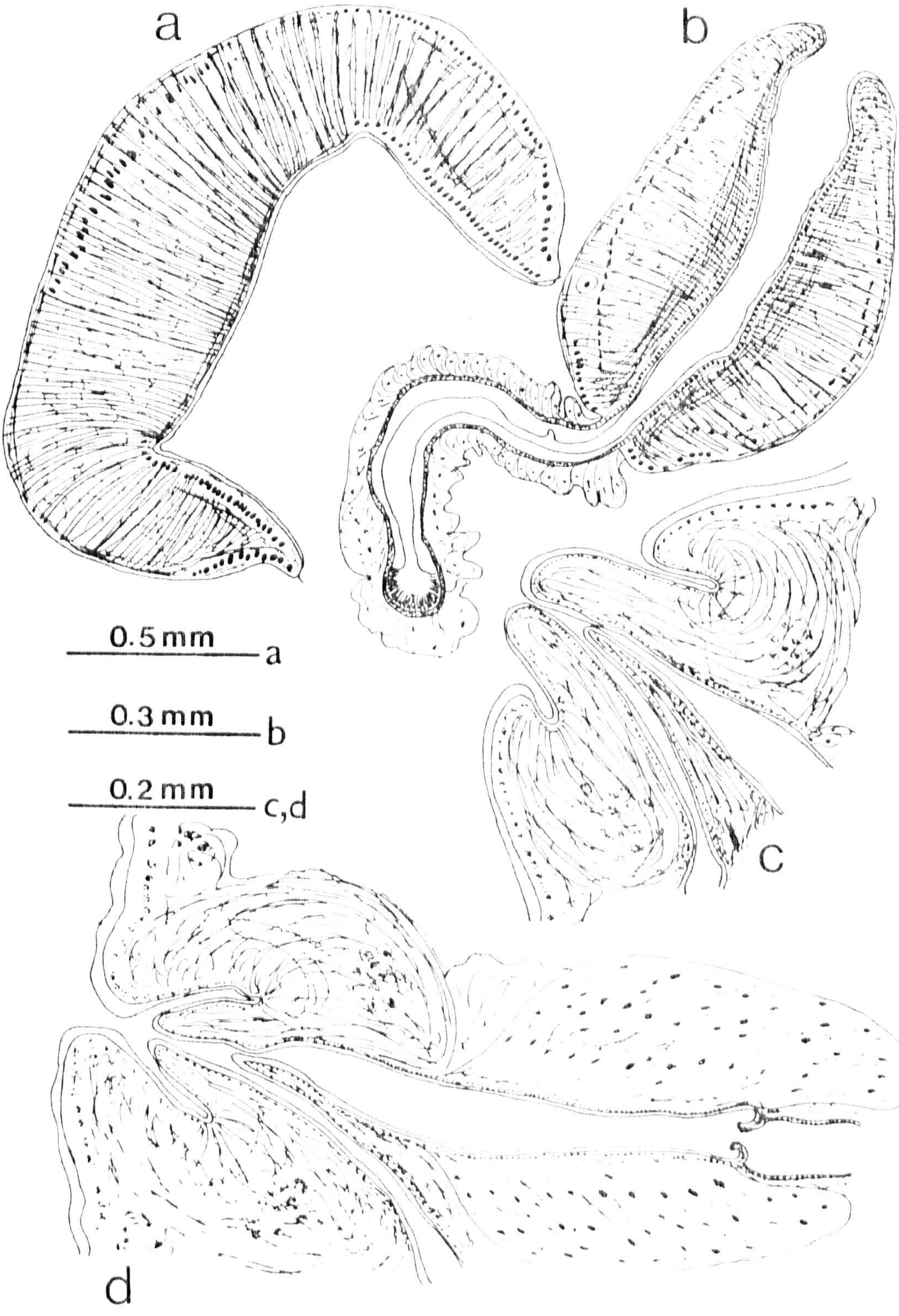
(median sagittal section)

a. Acetabulum (paramphistomum type)

b. Pharynx (calicophoron type) and oesophagus

c. Terminal genitalium (epiclitum type) with everted genital papilla

d. Terminal genitalium (epiclitum type) with retracted genital papilla


a
0.5 mm
a
0.3 mm
b
0.2 mm
c,d
b
c
d

Paramphistomum gotoi Fukui, 1922

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos taurus	Tokyo, Japan	Naturhistoriska riksmuseet (Stockholm) coll. no. 407, Nasmark's material.
	Batangas, Philippines	Author's own collection
Cattle	Rumania	Dr. Otto Sey
Bubalus bubalis	Egypt	Dr. Otto Sey
	Pangasinan, Philippines	Author's own collection
Sheep	Hong Kong	British Museum (Natural History) coll. no. 1928. 9.28.56.

HABITAT: Rumen

DESCRIPTION:

Body conical, may bend ventrally, 4.82-7.52 mm long, 1.54-2.48 mm in greatest width measured in the dorso-ventral direction; body surface has relatively large dome to block shaped papillae concentrated around the oral opening and ventrally from this point to the middle of the body and smaller papillae randomly arranged around the acetabular opening.

Acetabulum subterminal, external diameter 1.20-1.99 mm in the dorso-ventral direction; ratio to body length 1:3. to 1:6.9; of the paramphistomum type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 9-13; d.e.c.2, 25-33; d.i.c., 30-40; v.i.c., 41-45; v.e.c., 9-14; m.e.c., 17-23.

Pharynx 0.81-0.97 mm long, 0.65-1.15 mm wide in the dorso-ventral direction; ratio to body length 1:5.9 to 1:7.6, to the diameter of the acetabulum 1:1.4 to 1:1.9; of the liorchis type (sensu Näsmark, 1937) in median sagittal section; anterior two third of internal surface lined by long papillae. Oesophagus 0.70-1.05 mm long, usually bends dorsally; musculature of wall of moderate thickness, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, may be slightly wavy or almost straight in their course, reaching level of middle of acetabulum and blind ends curve to meet dorso-medially.

Testes deeply lobed, tandem in posterior half of the body; anterior testis 0.78-1.16 mm long; 0.90-0.99 mm wide in the dorso-ventral direction; posterior testis 0.47-0.98 mm long, 0.44-1.09 mm wide in the dorso-ventral direction; seminal vesicle long, strongly coiled and thin-walled; pars musculosa very short and weakly developed; pars prostatica relatively small.

Ovary subspherical, posttesticular, anterior and dorsal to acetabulum, 0.26-0.31 by 0.35-0.39 mm; Mehlis' gland close to ovary, 0.17-0.19 by 0.18-0.24 mm; Laurer's canal crosses excretory vesicle or duct and opens on the dorsal surface about 0.97-1.05 mm posteriorly to the excretory pore. Uterine coils very few, dorsal to testes and ventral to the male ducts; vitellaria in lateral fields, extend from level of pharynx to acetabulum, not confluent medially in their anterior or posterior limits; egg 136-140 by 70-73 µm.

Genital pore at level of oesophagus or its bifurcation; terminal genitalium of the gracile type (sensu Näsmark, 1937) in median sagittal section but with short genital papilla.

Excretory vesicle dorsal to acetabulum and posterior testis; excretory pore opens on the dorsal surface at level of the posterior border of anterior testis and anteriorly to Laurer's canal opening.

FIGURE 50

Paramphistomum gotoi Fukui, 1922

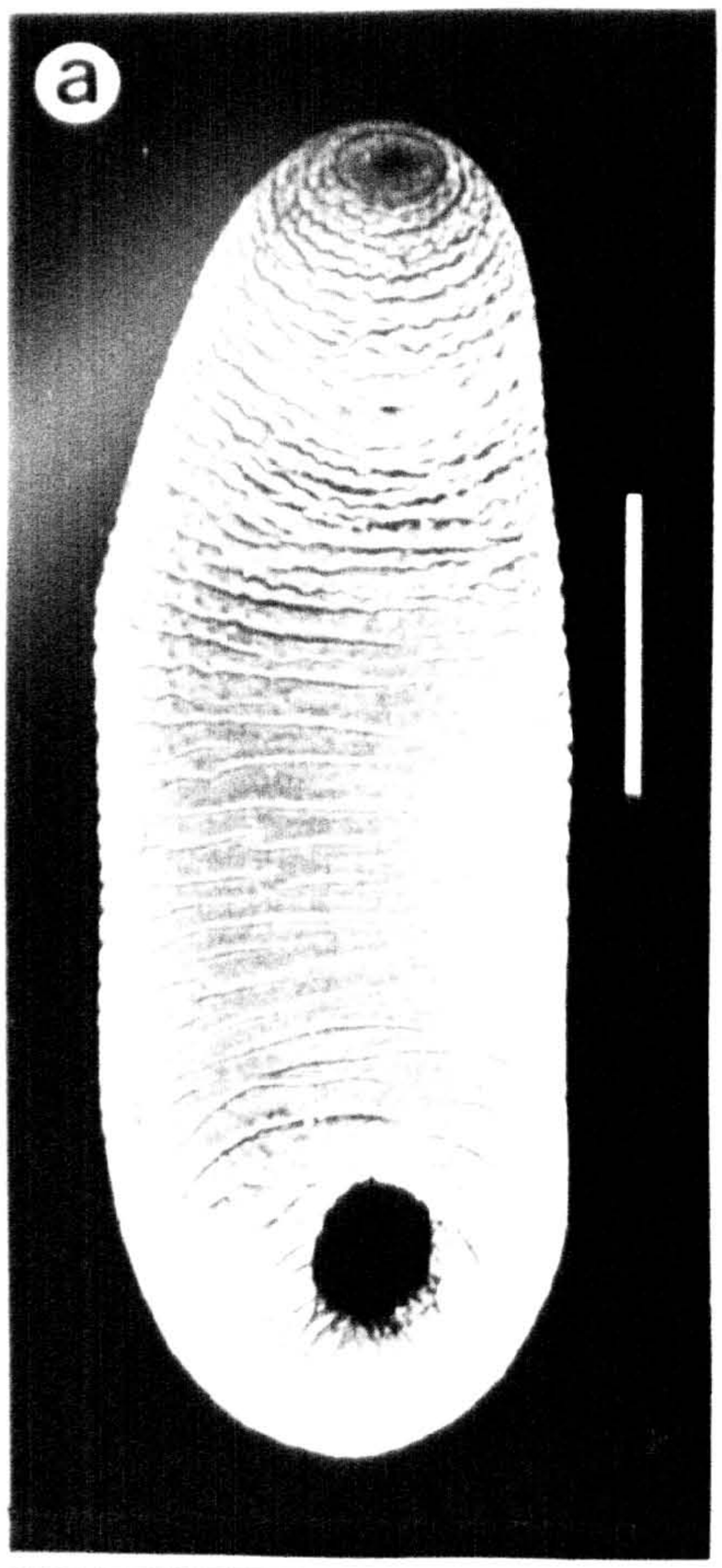
(SEM)

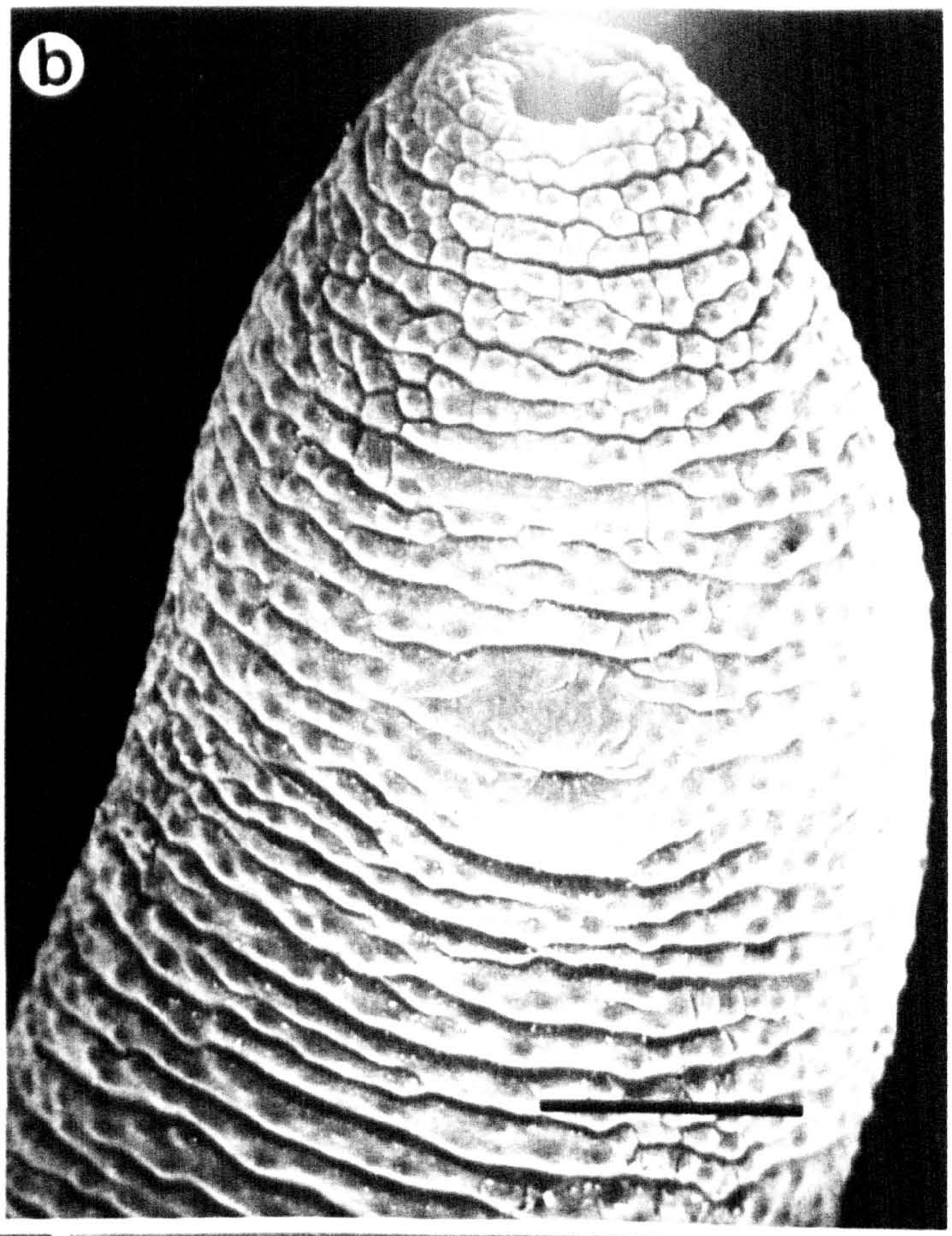
a. Whole worm, ventral view. Note papillae on anterior half (scale bar = 1 mm)

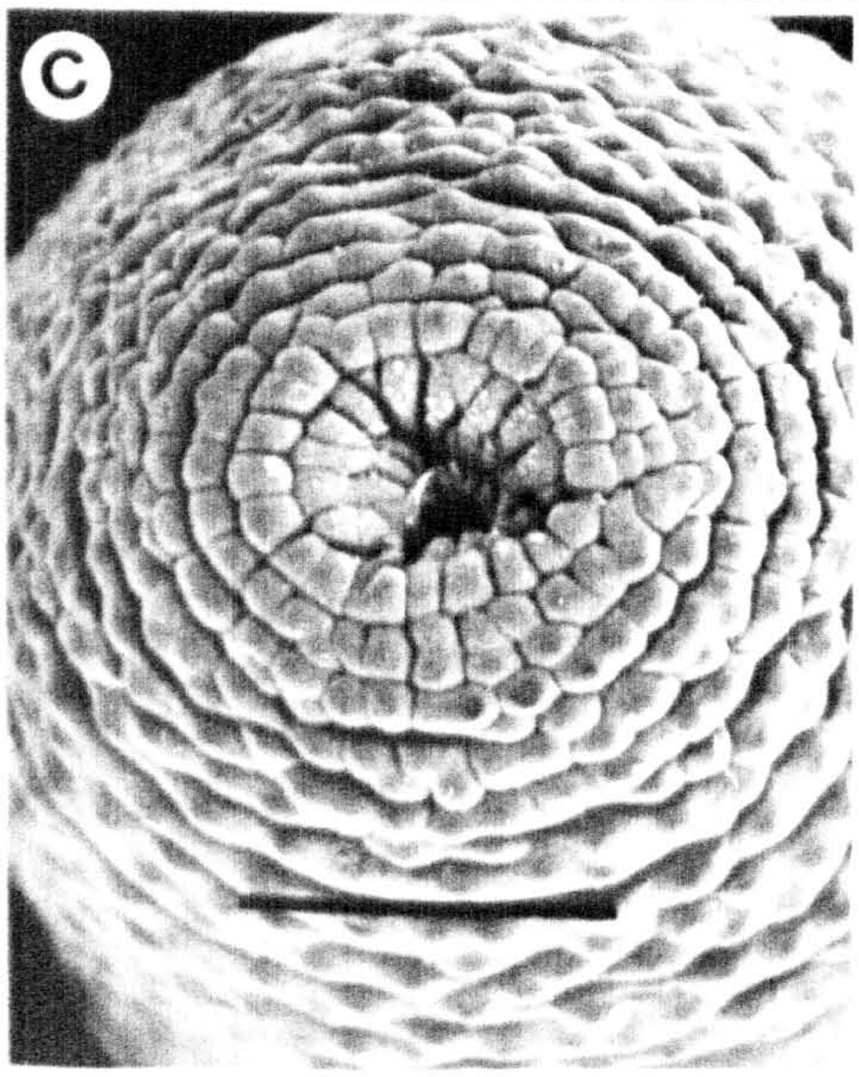
b. Anterior end arrangement of dome to block-shaped papillae around oral opening, end view (scale bar = 400 µm)

c. Anterior half showing genital pore region (scale bar = 300 µm)

d. Acetabular region, note much smaller, fewer and randomly arranged papillae (scale bar = 400 µm)


a


b


c

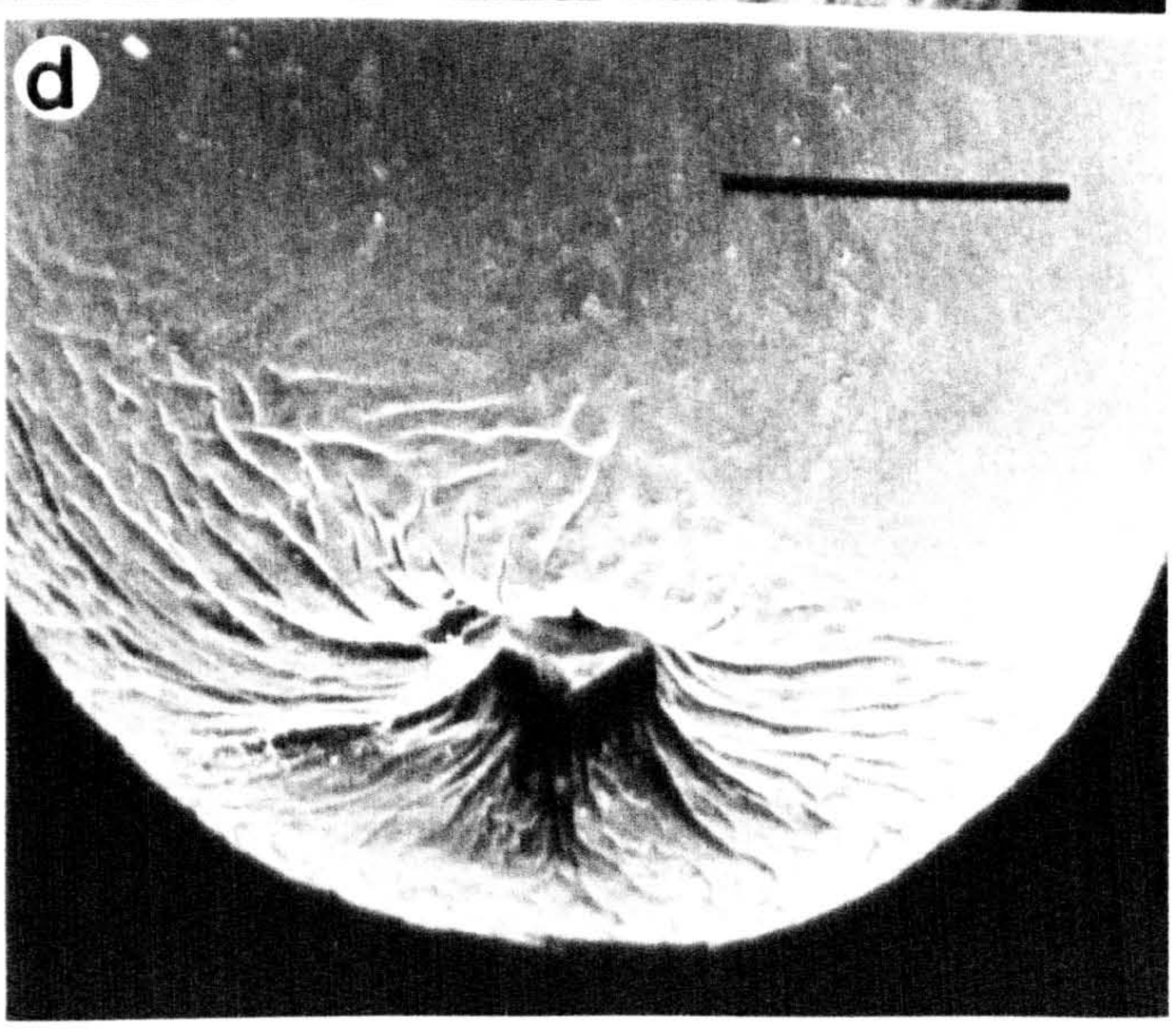

d

FIGURE 51

Paramphistomum gotoi Fukui, 1922

a. Whole worm, ventral view

b. Whole worm, sagittal view

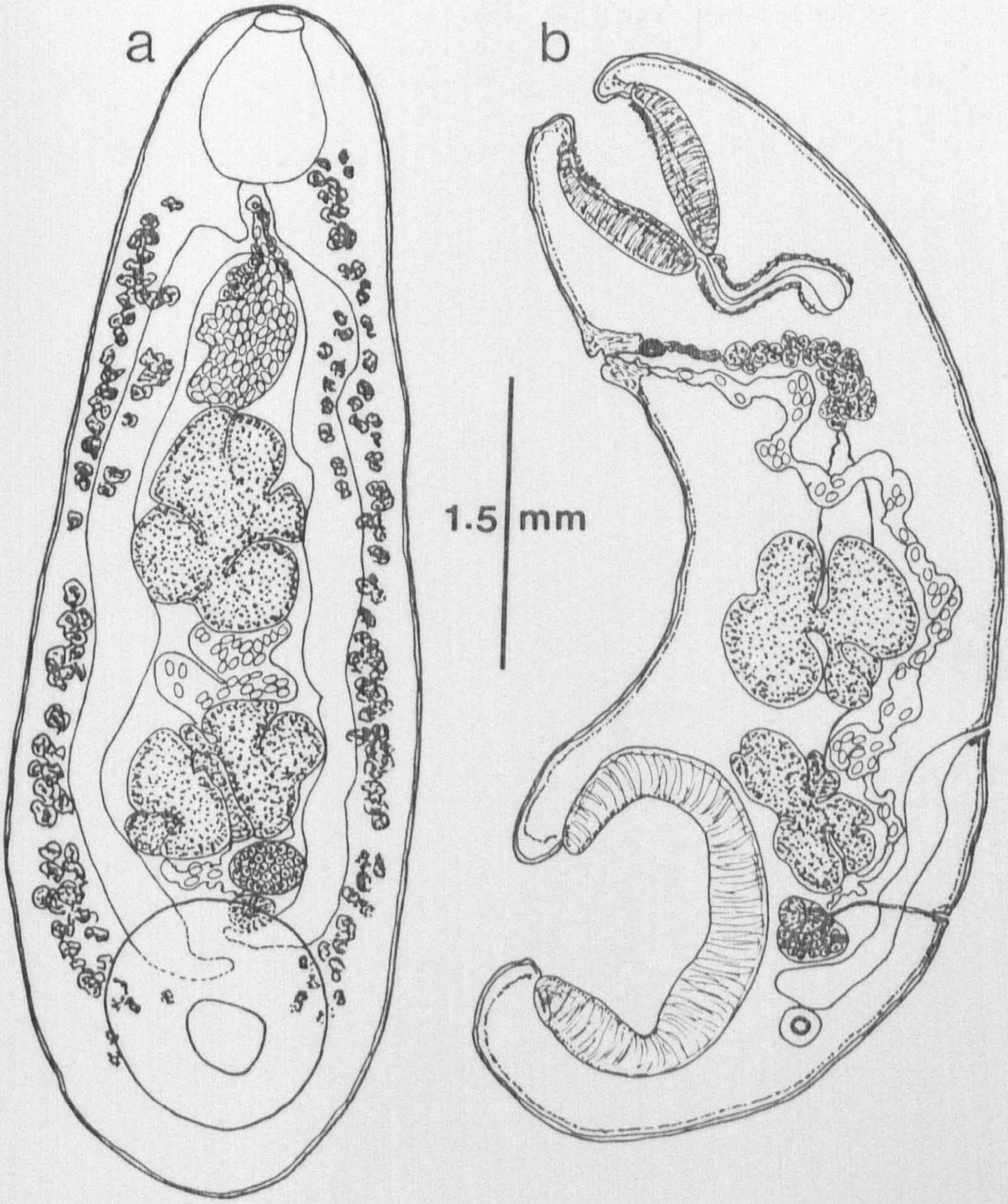

a
b
1.5 mm

FIGURE 52

Paramphistomum gotoi Fukui, 1922

(median sagittal section)

a. Acetabulum (paramphistomum type)

b. Pharynx (liorchis type) and oesophagus

c. Terminal genitalium (gracile type) and pars prostatica

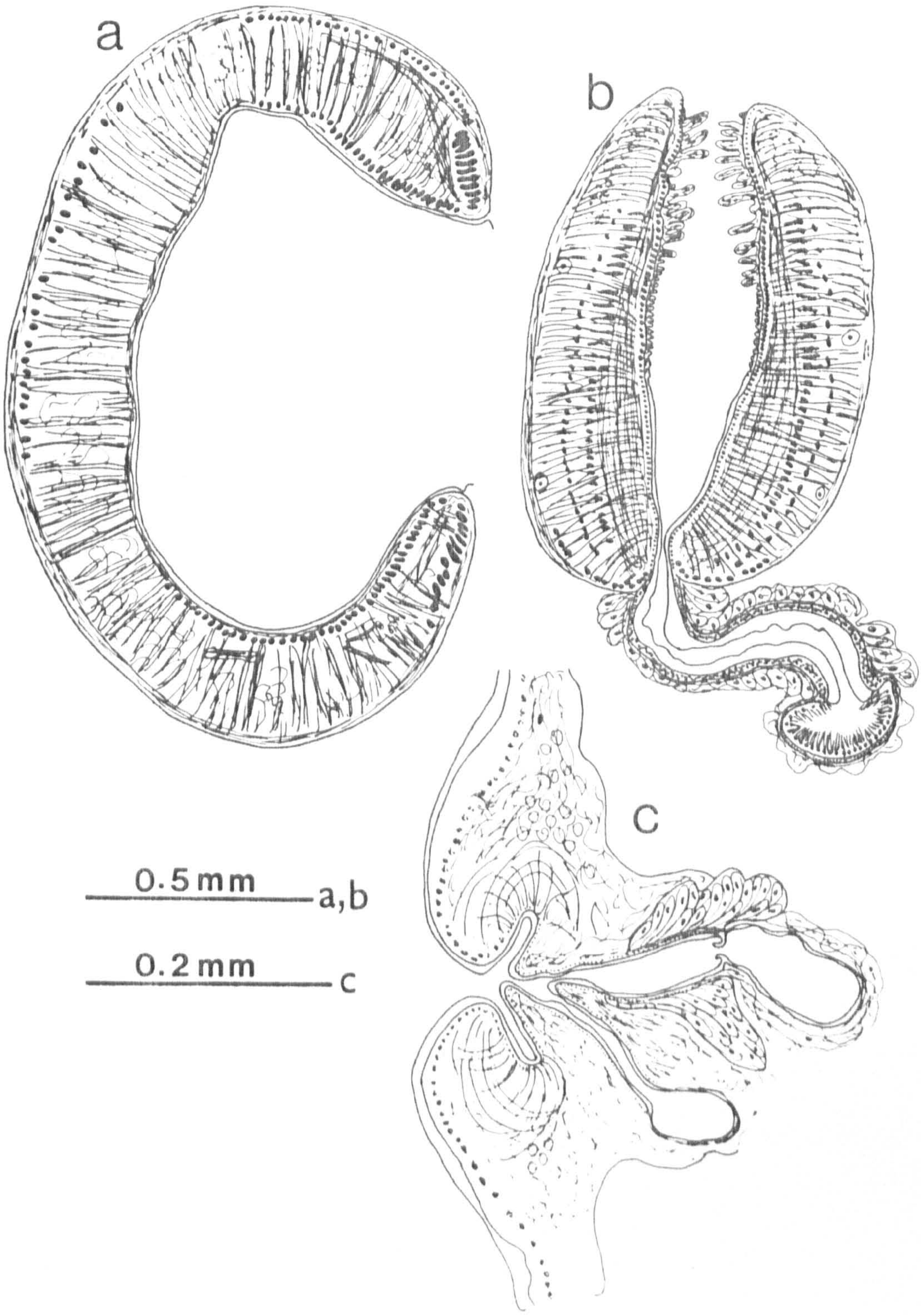

a
b
c
0.5mm
a,b
0.2mm
c

FIGURE 53

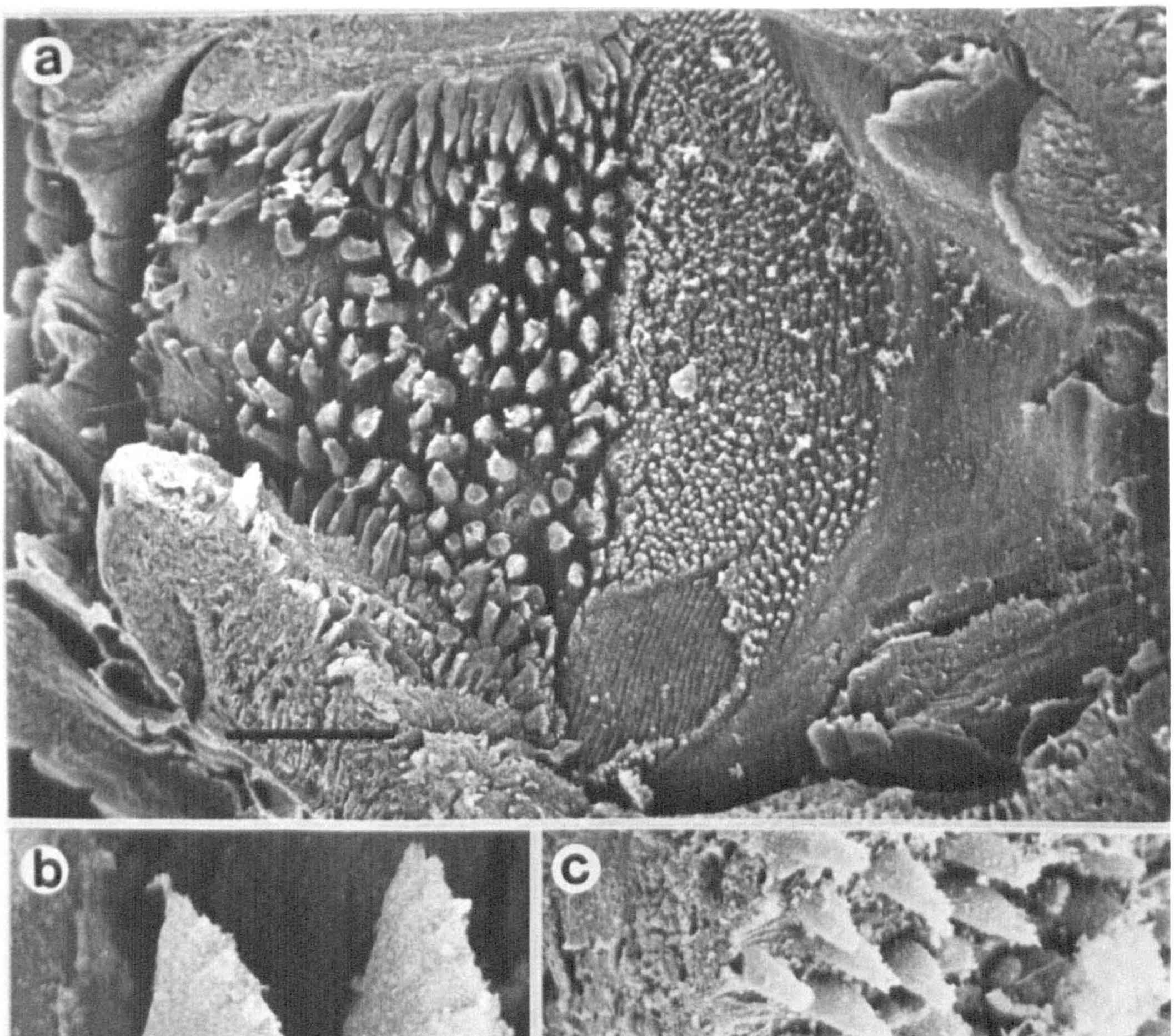
Paramphistomum gotoi Fukui, 1922

Internal surface of pharynx (SEM)

a. General view, note large papillae of two sizes on anterior two third of the surface (scale bar = 100 µm)

b. Closer view of longer papillae on anterior one third of the surface (scale bar = 15 µm)

c. Closer view of shorter papillae on middle third of the surface (scale bar = 15 µm)


a
b
c

Paramphistomum ichikawai Fukui, 1922

Synonym: Cotylophoron vigisi Davydova, 1963

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos taurus	Czechoslovakia	Dr. J. Pacenovsky
	Berlin, Germany	Prof. Dr. K. Odening
	Hannover, Germany	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Pusan, Korea	Dr. Jung-Kyun Chu
Cattle	Australia	Dr. K.C. Bremner
	U.S.S.R.	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Capra hircus	China	London School of Hygiene & Tropical Medicine

HABITAT: Rumen

DESCRIPTION:

Body conical, may bend ventrally, 4.9-9.49 mm long, 1.74-3.35 mm in greatest width in the dorso-ventral direction; body surface has small dome-shaped papillae which are present only on the anterior end around the oral opening and much smaller ones randomly arranged around the acetabular region.

Acetabulum subterminal, external diameter 1.16-1.66 mm in the dorso-ventral direction; ratio to body length 1:3 to 1:5.9; of the pisum type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 16-26; d.e.c.2, 8-14; d.i.c., 35-62; v.e.c., 18-26; v.i.c., 36-60; m.e.c., 15-20.

Pharynx 0.58-1.01 mm long, 0.48-0.87 mm wide in the dorso-ventral direction; ratio to body length 1:6.5 to 1:13.5, to the diameter of the acetabulum 1:1.3 to 1:2.6; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section; internal surface lined by small dome-shaped papillae. Oesophagus relatively short (0.33-0.50 mm long), nearly straight but may bend dorsally; musculature of wall of moderate thickness, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form irregular and shallow dorso-ventral bends, reach level of acetabulum with blind ends directed posteriorly.

Testes shallowy lobed, tandem in posterior two third of the body; anterior testis 0.43-1.19 mm long, 0.72-1.79 mm wide in the dorso-ventral direction; posterior testis 0.34-1.93 mm long, 1.18-2.10 mm wide in the dorso-ventral direction; seminal vesicle long, strongly coiled and thin-walled; pars musculosa short but relatively broad; pars prostatica relatively small.

Ovary 0.35-061 by 0.47-0.61 mm, dorsal to acetabulum and posterior to the testes; Mehlis' gland close to ovary, 0.20-0.53 by 0.44-0.53 mm; Laurer's canal crosses excretory vesicle or duct and opens on the dorsal surface about 0.45-0.68 mm posteriorly to the excretory pore. Uterine coils dorsal to testes and ventral to the male ducts; vitellaria in lateral fields, extensive from level of pharynx to level of acetabulum, sometimes encroaching to intercaecal region, anterior limit confluent dorso-medially; egg 123-129 by 64-70 µm.

Genital pore at a level posterior to oesophageal bifurcation about 0.41-0.53 posterior to it; terminal genitalium of the ichikawai type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to ovary, Mehlis' gland and posterior testis; excretory pore opens on the dorsal surface at level of the posterior border of anterior testis and anteriorly to the Laurer's canal opening.

FIGURE 54

Paramphistomum ichikawai Fukui, 1922

(SEM)

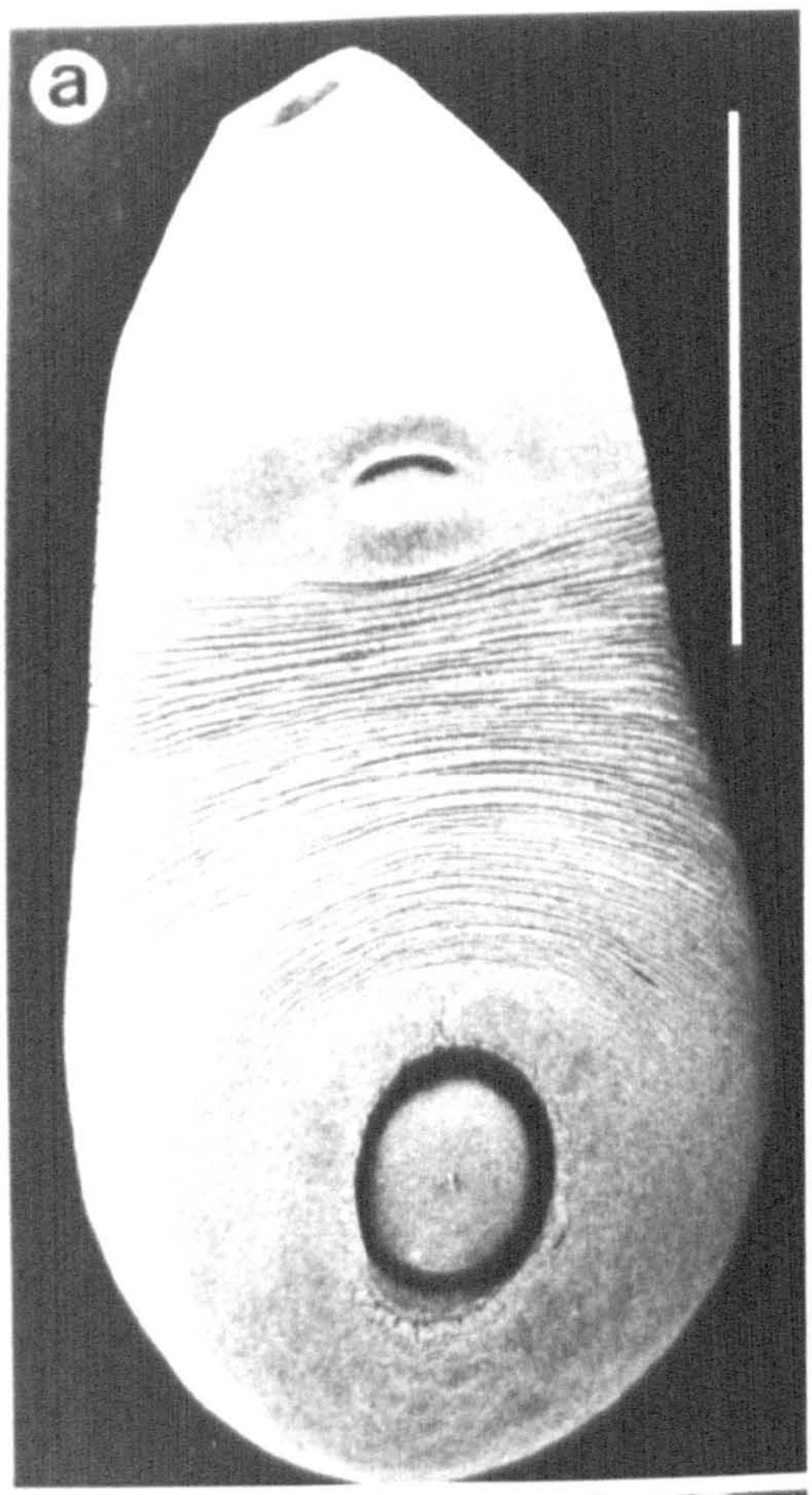
a. Whole worm, ventral view (scale bar = 1 mm)

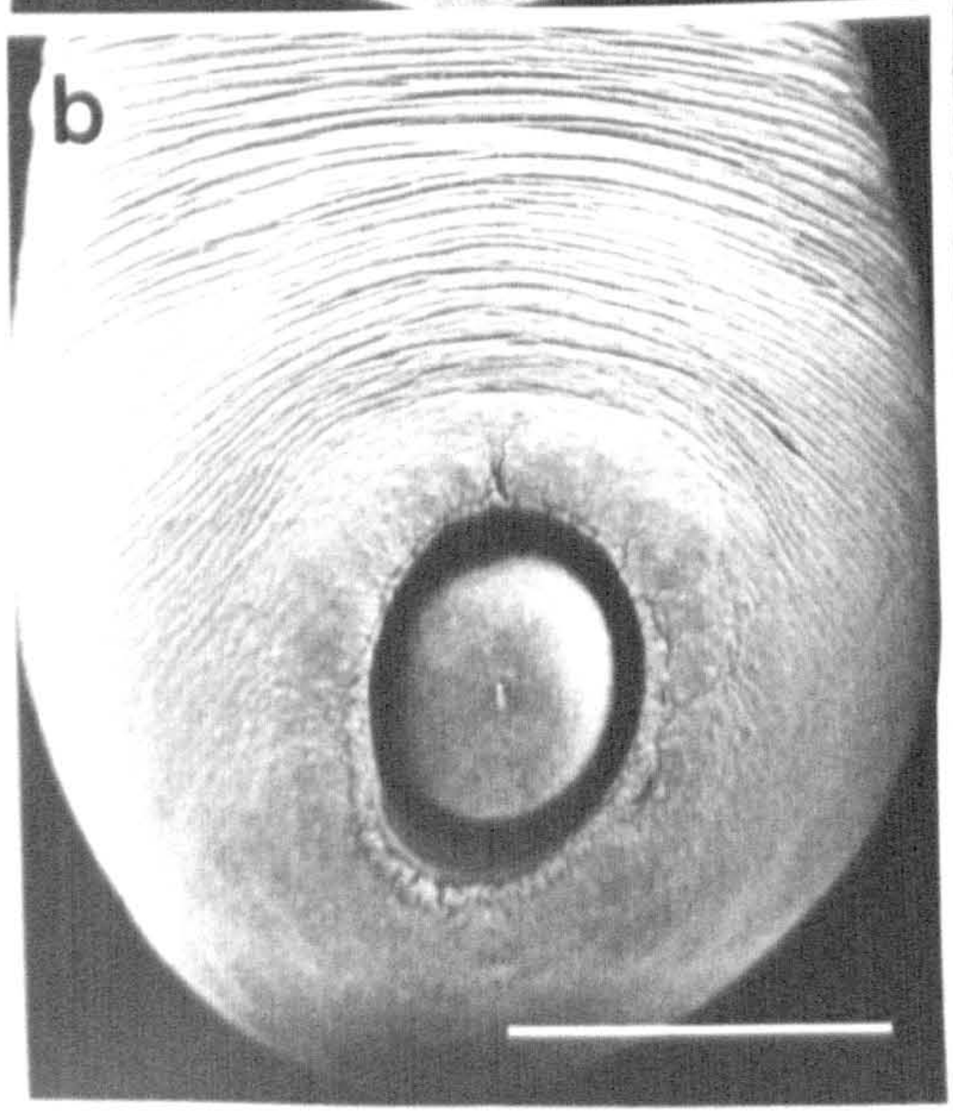
b. Acetabular region, note very small and few papillae randomly arranged (scale bar = 500 µm)

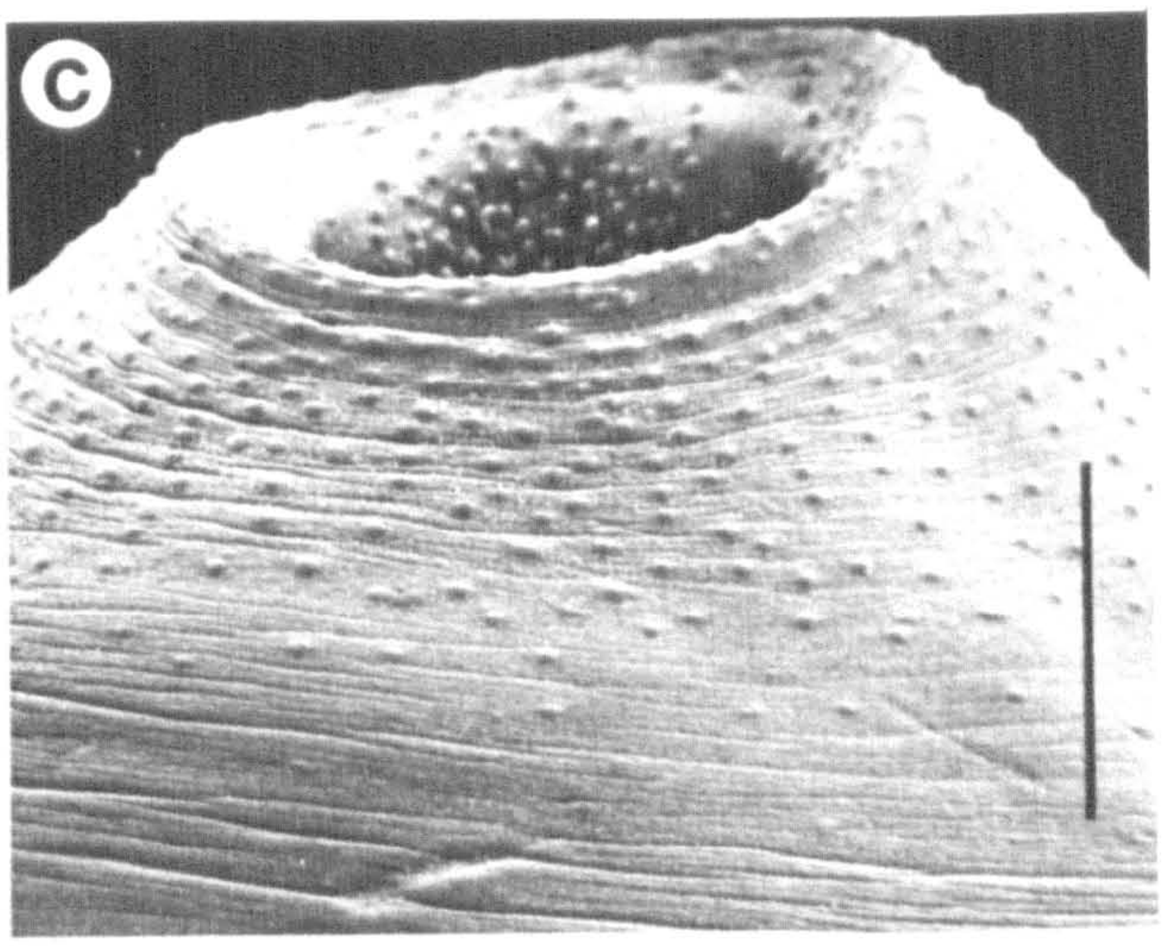
c. Anterior end showing larger papillae (scale bar = 150 µm)

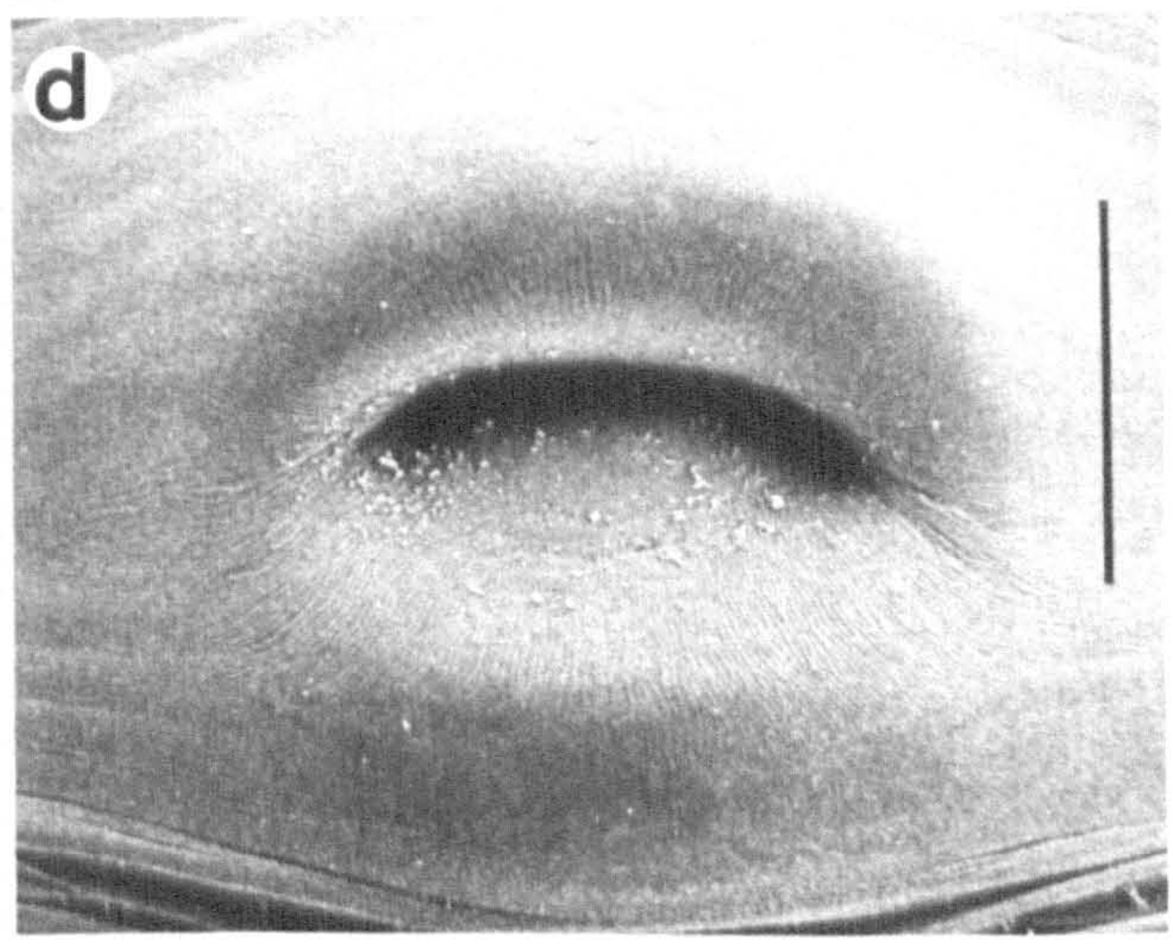
d. Genital pore region (scale bar = 50 µm)

e. Closer view of genital pore wall showing fine ridges (scale bar = 3 µm)


a


b


c


d

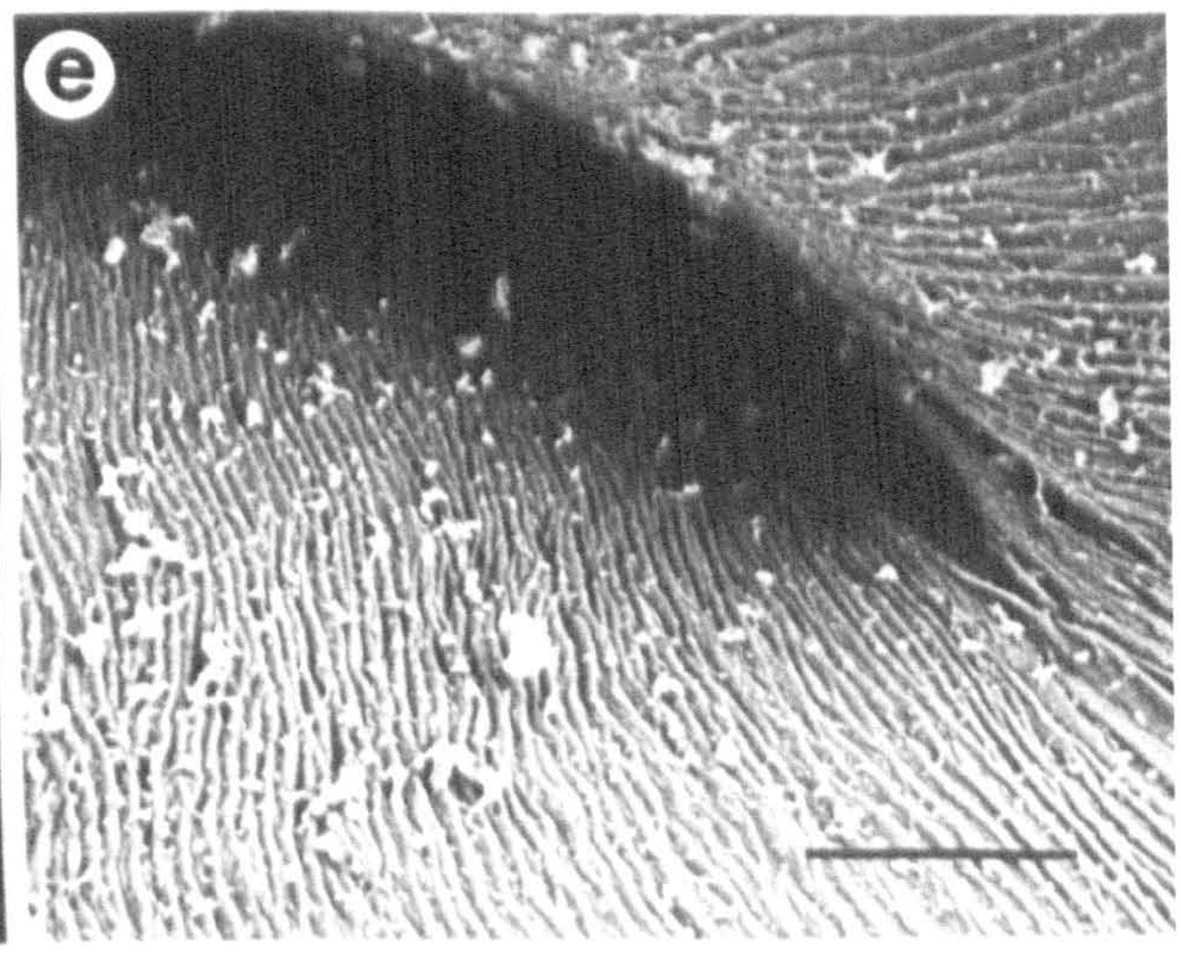

e

FIGURE 55

Paramphistomum ichikawai Fukui, 1922

a. Whole worm, ventral view

b. Whole worm, sagittal view

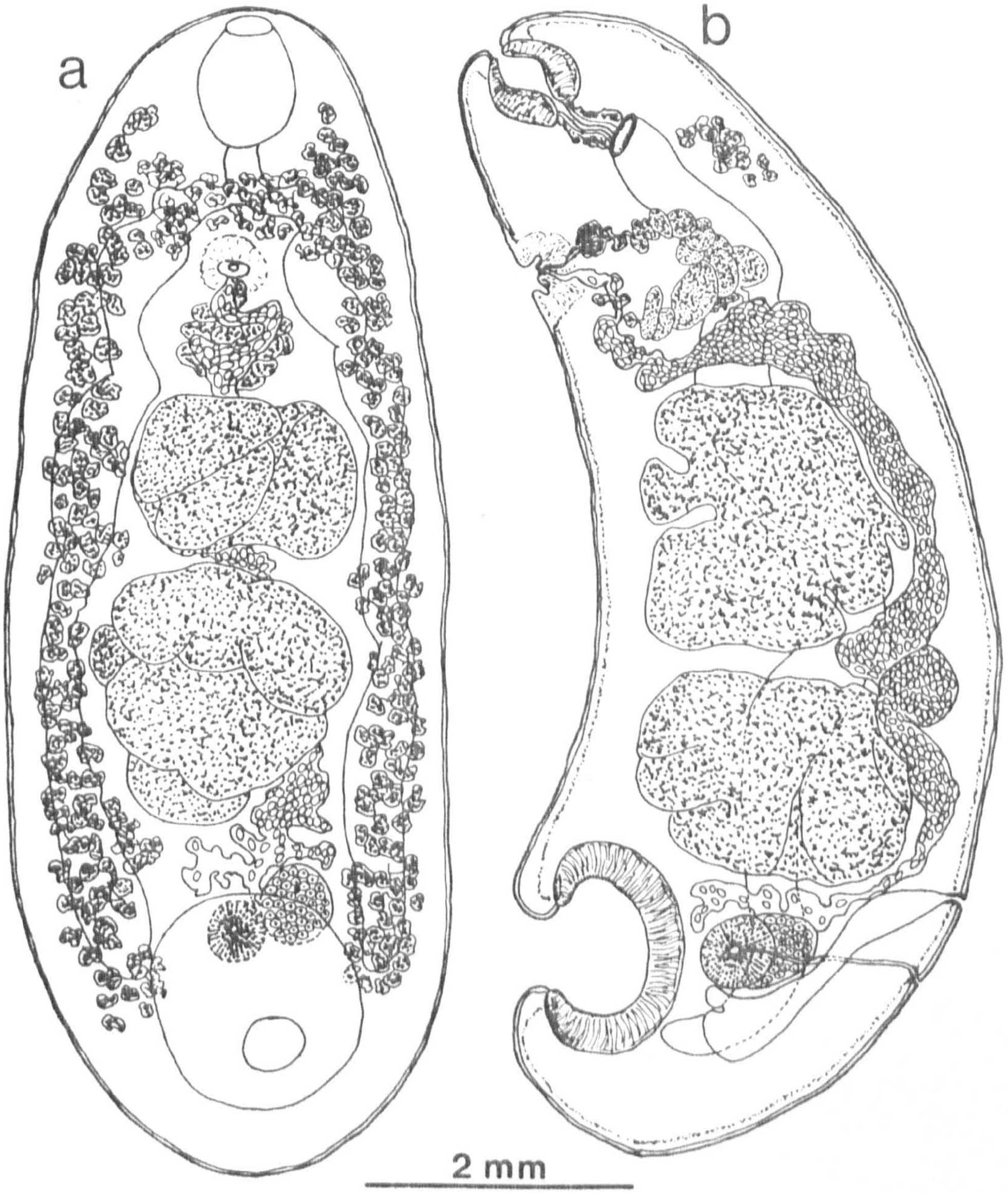

a
b
2 mm

FIGURE 56

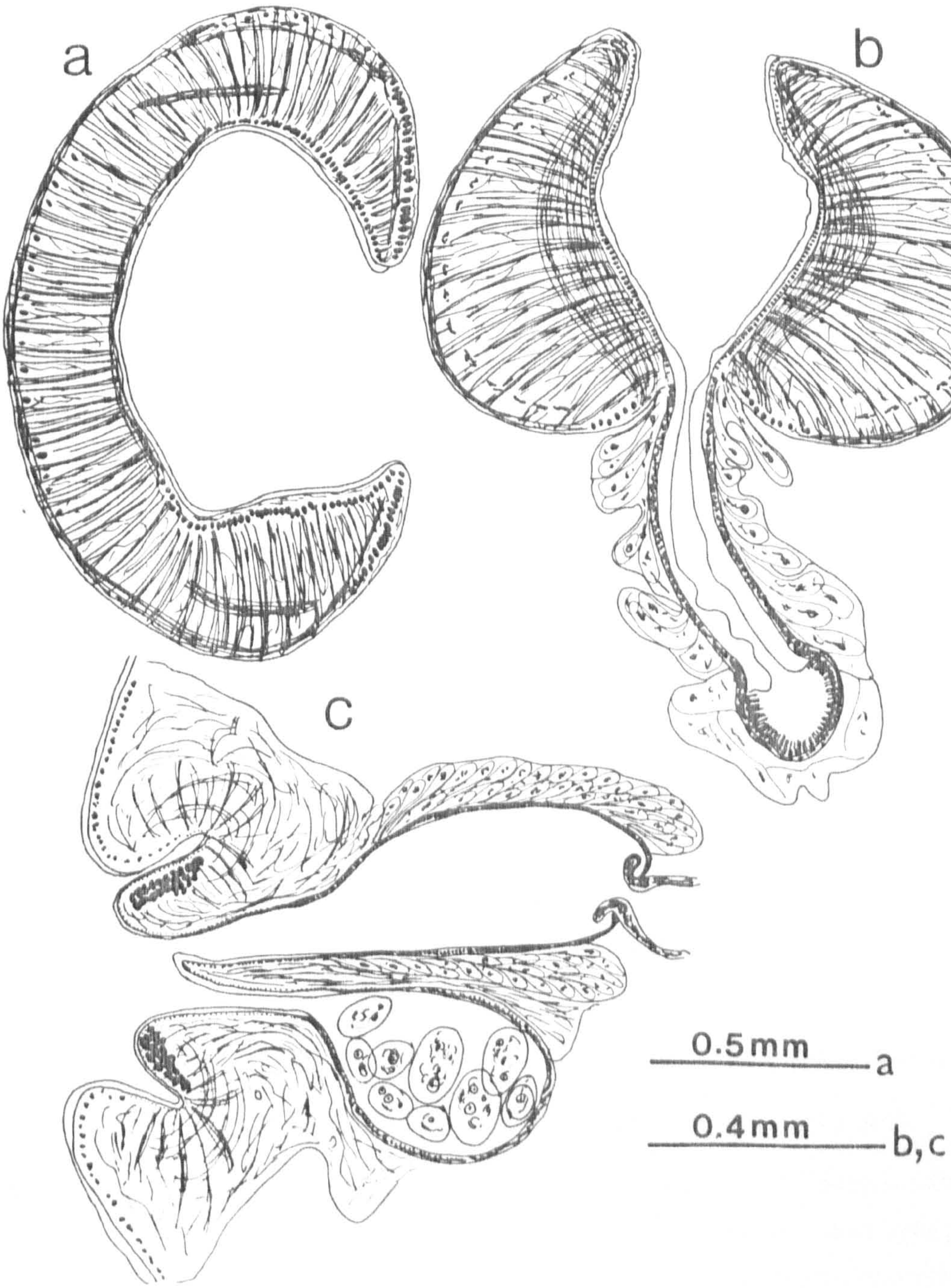
Paramphistomum ichikawai Fukui, 1922

(median sagittal section)

a. Acetabulum (pisum type)

b. Pharynx (calicophoron type) and oesophagus

c. Terminal genitalium (ichikawai type) and pars prostatica


a
b
c
0.5mm
a
0.4mm
b,c

Paramphistomum leydeni Näsmark, 1937

Synonyms: Paramphistomum scotiae Willmott, 1950
Paramphistomum julimarinorum Velazquez-Maldonado, 1976
Paramphistomum nicabrasilorum Velazquez-Maldonado, 1976
Paramphistomum procapri Wang, 1979
Cotylophoron skrjabini Mitskevich, 1959 in part

TYPE SPECIMENS: Naturhistoriska riksmuseet, Stockholm (co-types), Bos taurus, Ritsema

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos taurus	Hannover, Germany	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Turkey	Prof. Dr. Fakhri Sayin
	U.S.S.R.	London School of Hygiene & Tropical Medicine coll. no. 1955.
Cattle	Brazil	Prof. J.J.F. Miranda
	Utrecht, Netherlands	London School of Hygiene & Tropical Medicine, LeRoux collection.
	U. Skraastad, Norway	Dr. Oddvar Helle
	Ankara, Turkey	Prof. Dr. Nevzat Güralp
	Venezuela	Prof. J.J.F. Miranda
Cervus elaphus	Austria	Institut für Parasitologie und Allgemeine Zoologie, Veterinärmedizinische Universität (Vienna) coll. no. 1/6/258, presented by Dr. H. Prosl.

HABITAT: Rumen and reticulum

DESCRIPTION:

Body conical, bends ventrally, 4.10-6.80 mm long, 2.00-3.35 mm in greatest width in the dorso-ventral direction; body surface has dome-shaped papillae concentrated around the oral opening and ventrally from this point to the middle of the body.

Acetabulum subterminal; external diameter 1.28-1.81 mm in the dorso-ventral direction; ratio to body length 1:3 to 1:3.7; of the paramphistomum type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 10-14; d.e.c.2, 34-39; d.i.c., 38-44; v.e.c., 16-20; v.i.c., 47-50; m.e.c., 14-26.

Pharynx 0.57-0.84 mm long; 0.51-0.58 mm wide in the dorso-ventral direction; ratio to body length 1:6 to 1:8.6, to the diameter of the acetabulum 1:1.9 to 1:2.5; of the liorchis type (sensu Näsmark, 1937) in median sagittal section; anterior two third of internal surface lined by long papillae. Oesophagus 0.51-0.78 mm long, may bend dorsally; musculature of wall moderate in thickness, no bulb or posterior sphincter; lumen lined by thick hyaline layer throughout its length. Caeca in lateral sides of the body, form shallow dorso-ventral bends but may be almost straight in their course, reach level of acetabulum with blind ends slightly curved dorsally but do not meet medially.

Testes shallowy lobed, tandem in posterior two third of the body, appear wedge-shaped dorso-ventrally; anterior testis 0.53-0.97 mm long, 1.01-1.54 mm in the dorso-ventral direction; posterior testis 0.53-0.93 mm long, 0.83-1.96 mm in the dorso-ventral direction. Seminal vesicle long, strongly coiled and thin-walled; pars musculosa short and weakly developed; pars prostatica small, 0.19-0.32 by 0.18-0.33 mm in size.

Ovary posttesticular and dorsal to acetabulum, 0.28-0.55 by 0.28-0.69 mm; Mehlis' gland close to or immediately posterior to ovary, 0.23-0.38 by 0.19-0.44 mm; Laurer's canal crosses excretory vesicle or duct, opens on the dorsal surface about 0.57-1.06 mm posteriorly to the excretory pore; uterine coils dorsal to testes and ventral to the male ducts; vitellaria in lateral fields, extend from level of pharynx to anterior level of acetabulum, not confluent medially in their anterior or posterior limits; egg 145-150 by 75-78 µm.

Genital pore at level of pharynx or immediately posterior to oesophageal bifurcation; terminal genitalium of the leydeni type (new type) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland and posterior to posterior testis; excretory pore opens on the dorsal surface at level of the posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 57

Paramphistomum leydeni Näsmark, 1937

(SEM)

a. Whole worm, ventral view. Note large papillae on anterior half (scale bar = 500 µm)

b. Anterior half showing genital pore region and distribution of papillae (scale bar = 200 µm)

c. Oral end showing arrangement of papillae (scale bar = 100 µm)

d. Acetabular region (scale bar = 500 µm)

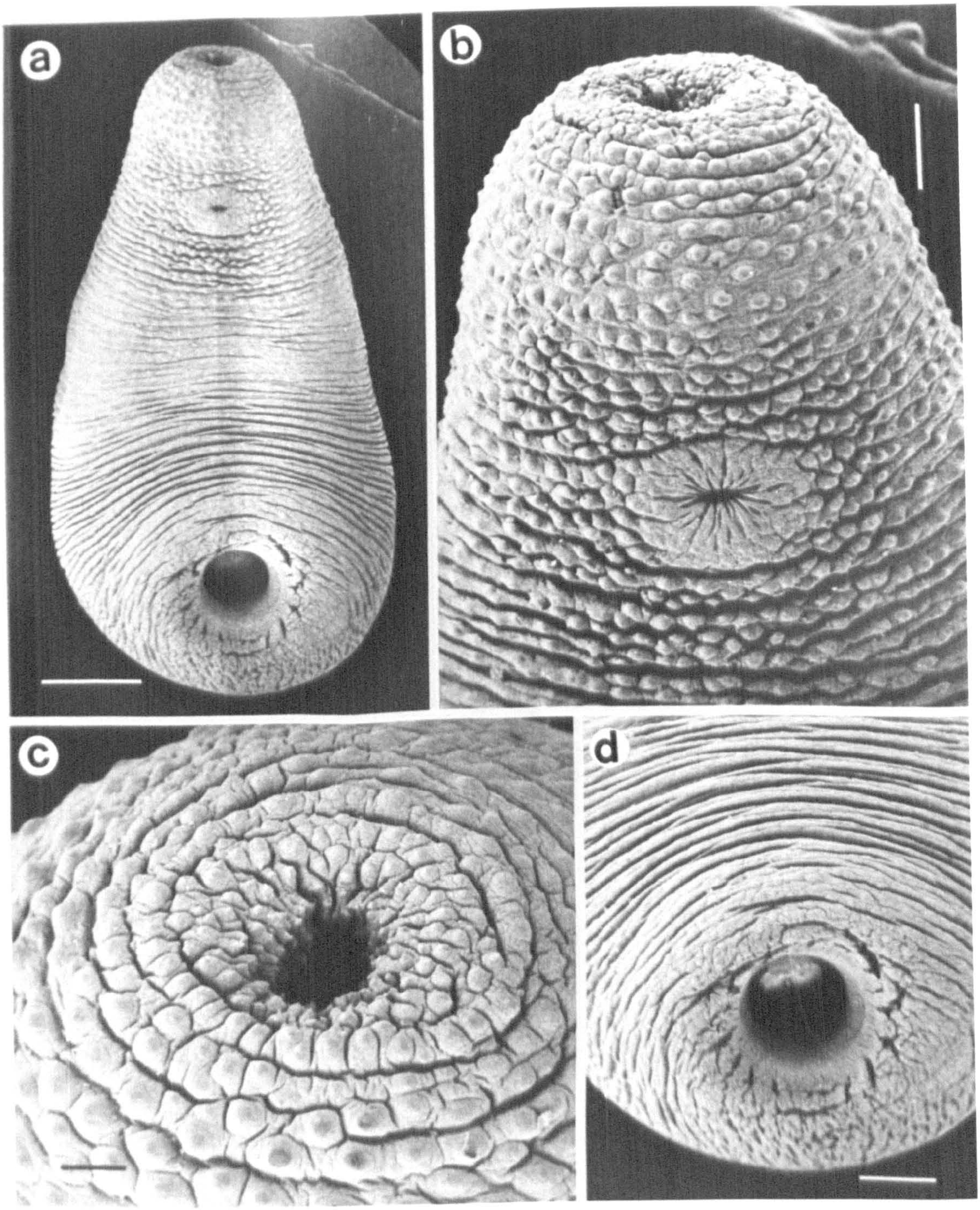

a
b
c
d

FIGURE 58

Paramphistomum leydeni Näsmark, 1937

a. Whole worm, ventral view

b. Whole worm, sagittal view

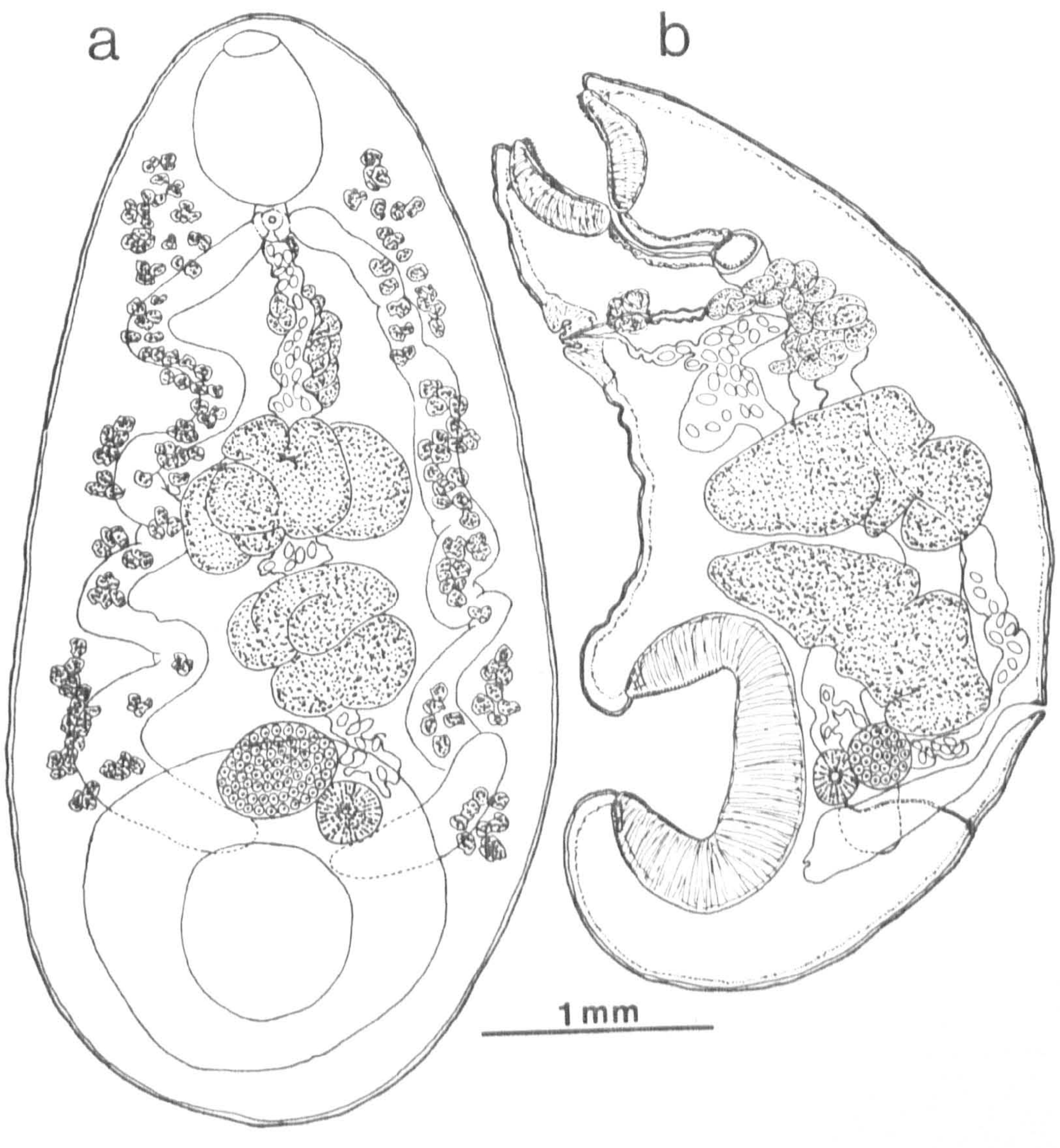

a
b
1 mm

FIGURE 59

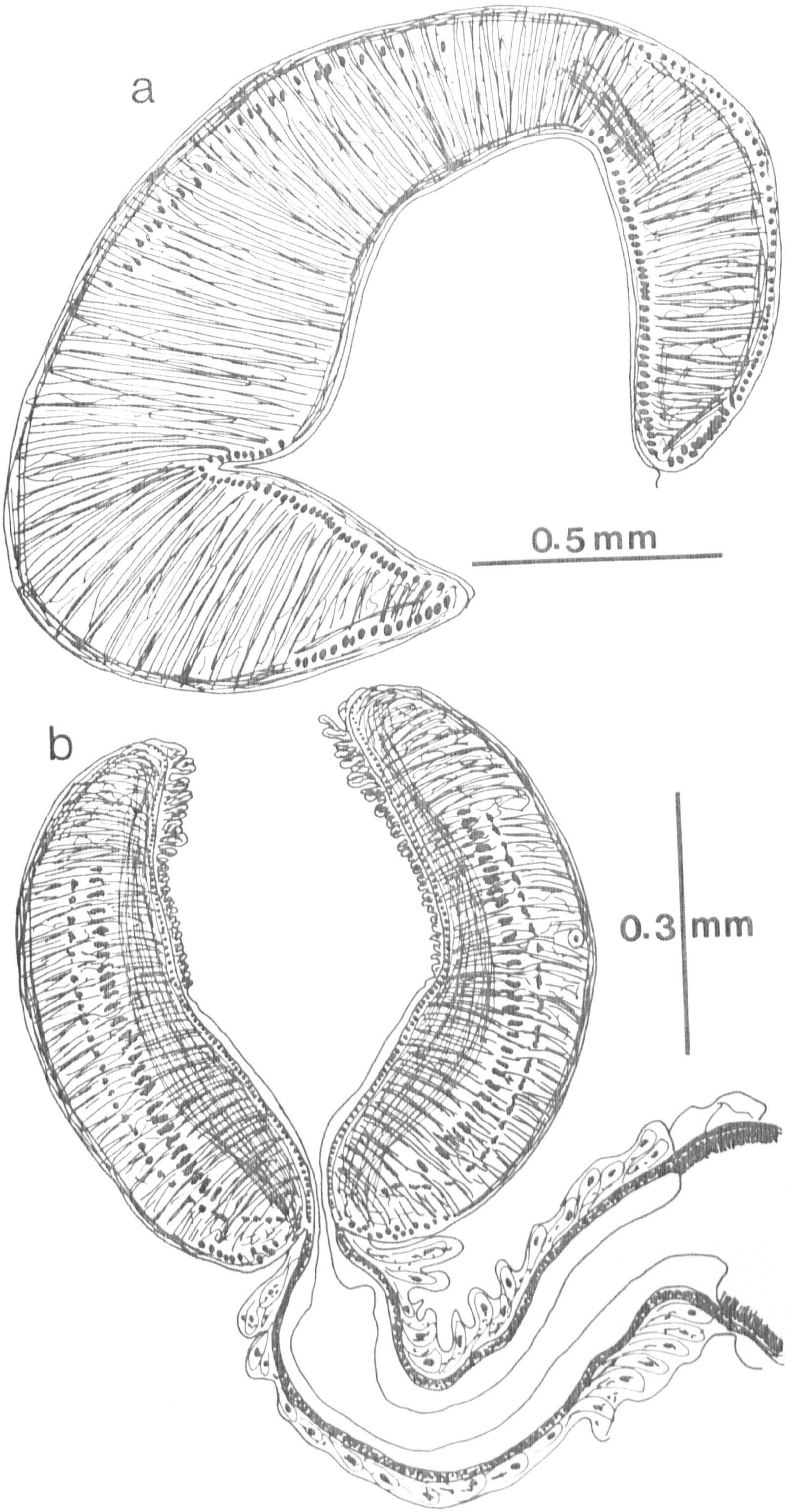
Paramphistomum leydeni Näsmark, 1937

(median sagittal section)

a. Acetabulum (paramphistomum type)

b. Pharynx (liorchis type) and oesophagus

a



0.5 mm

b

0.3 mm

FIGURE 60

Paramphistomum leydeni Näsmark, 1937

Various forms of the terminal genitalium (leydeni type)
(median sagittal section)

a. Well relaxed specimen and showing also the pars prostatica

b. Contracted specimen with extruded genital papilla

c. Contracted specimens with retracted genital papilla

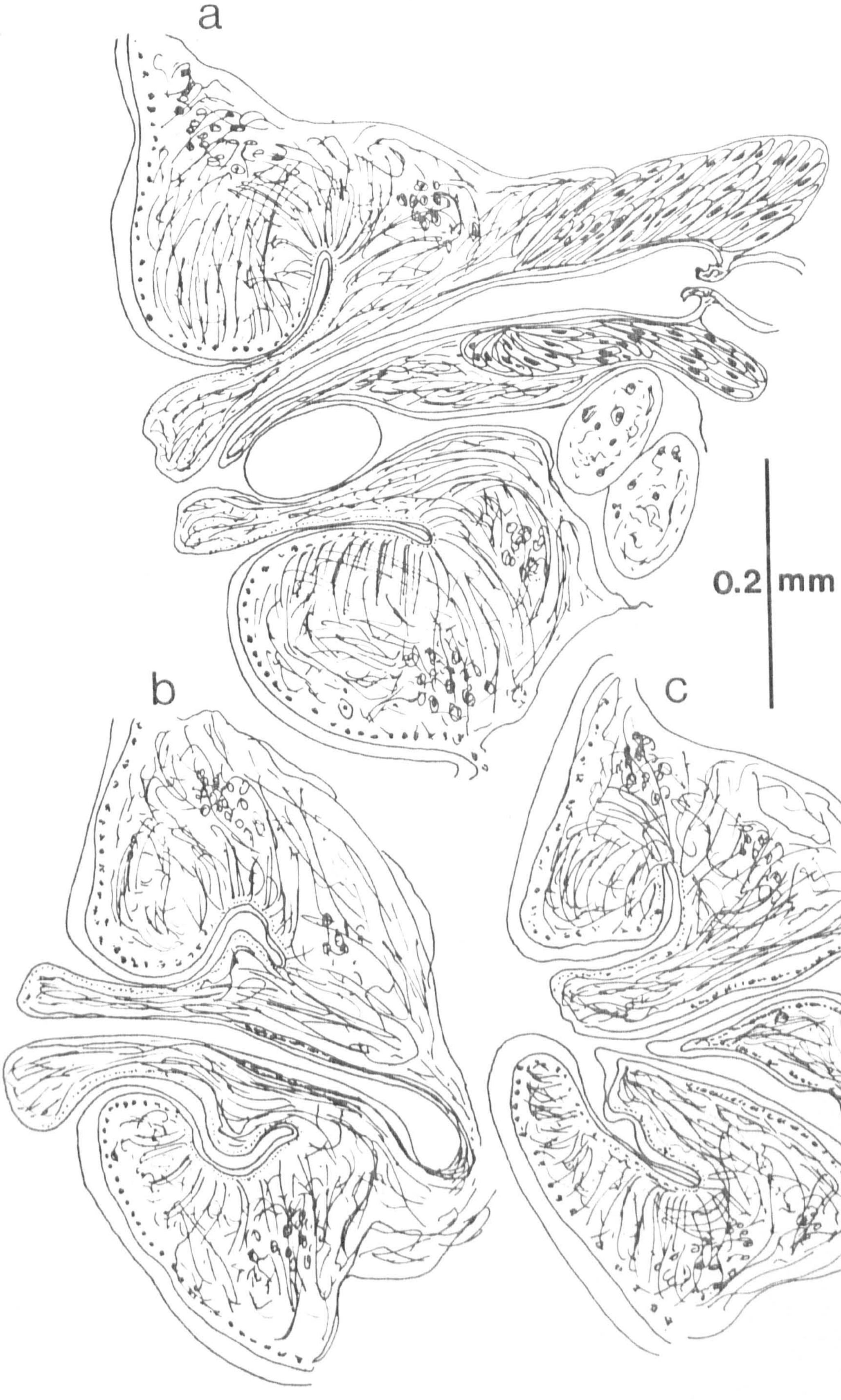

a
b
c
0.2 mm

FIGURE 61

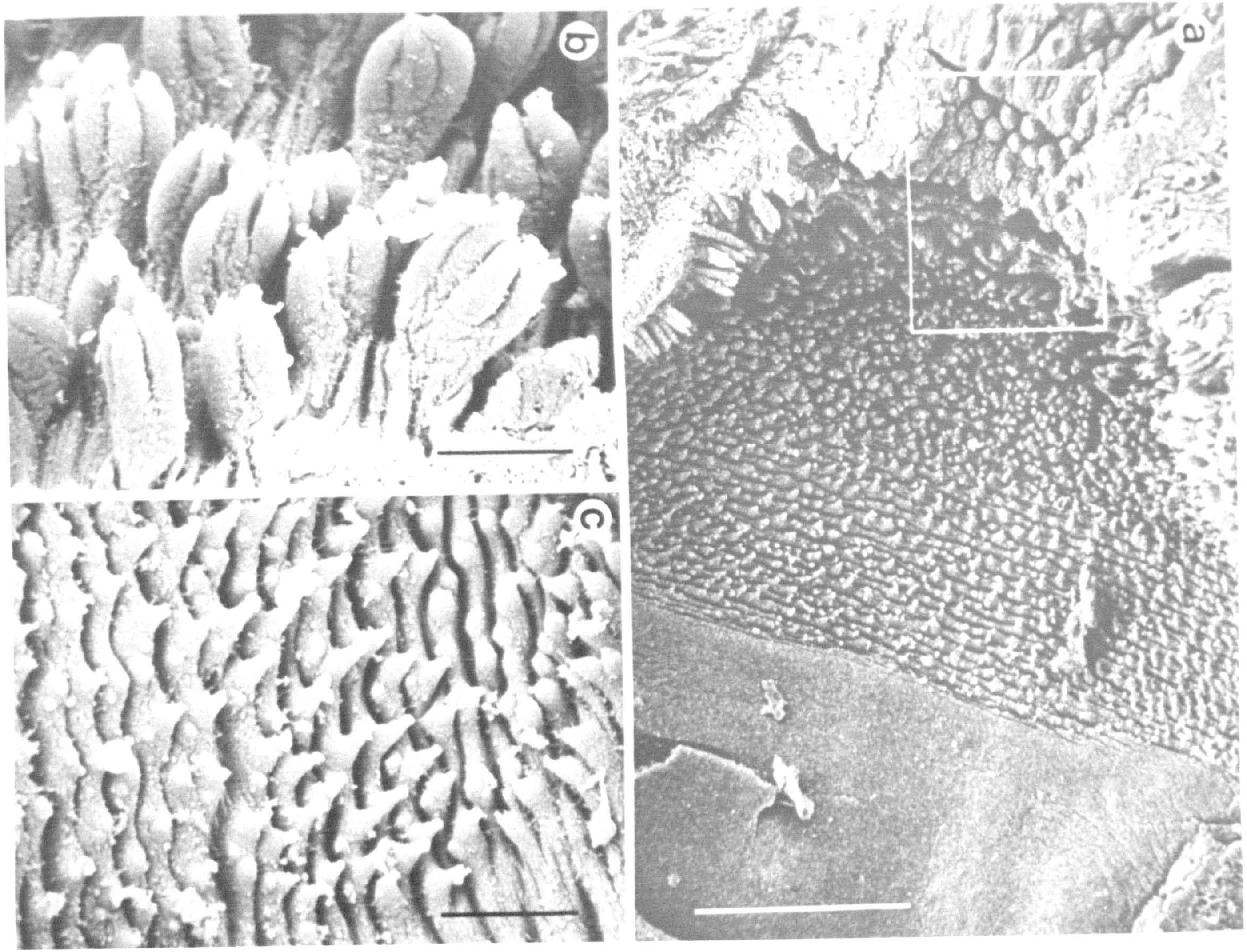
Paramphistomum leydeni Näsmark, 1937

Internal surface of pharynx (SEM)

a. General view, note large papillae of two sizes on anterior two third of the surface (scale bar = 100 µm)

b. Closer view of longer papillae on anterior third of surface (scale bar = 15 µm)

c. Closer view of shorter papillae on middle third of surface (scale bar = 15 µm)


a
b
c

Paramphistomum hiberniae Willmott, 1950

TYPE SPECIMENS: London School of Hygiene and Tropical Medicine, type collection numbers 332-338 (sagittal section) and 331 (whole mount, co-type), Bos taurus Scotland.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos taurus	England	Commonwealth Institute of Helminthology coll. no. 965.
	Ireland	London School of Hygiene & Tropical Medicine coll. no. 5275.

HABITAT: Rumen

DESCRIPTION:

Body conical, almost straight but may bend ventrally, 4.50-11.40 mm long, 1.76-4.01 mm in greatest width in the dorso-ventral direction; body surface has dome-shaped papillae concentrated around the oral opening and ventrally from this point to about the middle of the body.

Acetabulum subterminal; external diameter 1.48-2.36 mm in the dorso-ventral direction; of the paramphistomum type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 10-20; d.e.c.2, 28-36; d.i.c., 32-48; v.e.c., 11-22; v.i.c., 46-55; m.e.c., 2-8.

Pharynx 0.60-0.98 mm long, 0.46-0.82 mm wide in the dorso-ventral direction; ratio to body length 1:6.8 to 1:10.8, to the diameter of the acetabulum 1:2.2 to 1:3; of the liorchis type (sensu Näsmark, 1937) in median sagittal section; anterior two third of internal surface lined by long papillae. Oesophagus 0.48-0.95 mm

long, slightly bend dorsally; musculature of wall moderate in thickness, no bulb or posterior sphincter; internal surface lined by hyaline layer throughout its length. Caeca in lateral sides of the body, almost straight, may or may not reach level of acetabulum and blind ends slightly directed dorsally.

Testes small, deeply lobed, tandem with some distance from each other in the posterior two third of the body; anterior testis 0.60-0.81 mm long, 0.60-0.98 mm in the dorso-ventral direction; posterior testis 0.62-0.80 mm long, 0.77-1.27 mm in the dorso-ventral direction. Seminal vesicle moderate in length, coiled and thin-walled; pars musculosa short and weakly developed; pars prostatica small.

Ovary subspherical, in between testes and acetabulum, 0.23-0.72 by 0.51-0.68 mm: Mehlis' gland close to ovary, 0.18-0.45 by 0.33-0.68 mm; Laurer's canal crosses excretory vesicle or duct, opens on the dorsal surface about 0.60-0.66 mm posteriorly to the excretory pore. Uterine coils dorsal to testes and ventral to the male ducts; vitellaria in lateral fields, may encroach in the intercaecal region, extend from posterior border of pharynx to acetabulum, anterior limit confluent dorso-medially; egg 142-150 by 73-79 µm.

Genital pore at level of oesophagus; terminal genitalium of the leydeni type (new type) in median sagittal section.

Excretory vesicle large, extends dorsally from level of posterior border of posterior testis to posterior border of acetabulum; excretory pore opens on the dorsal surface at level of posterior border of posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 62

Paramphistomum hiberniae Willmott, 1950

(SEM)

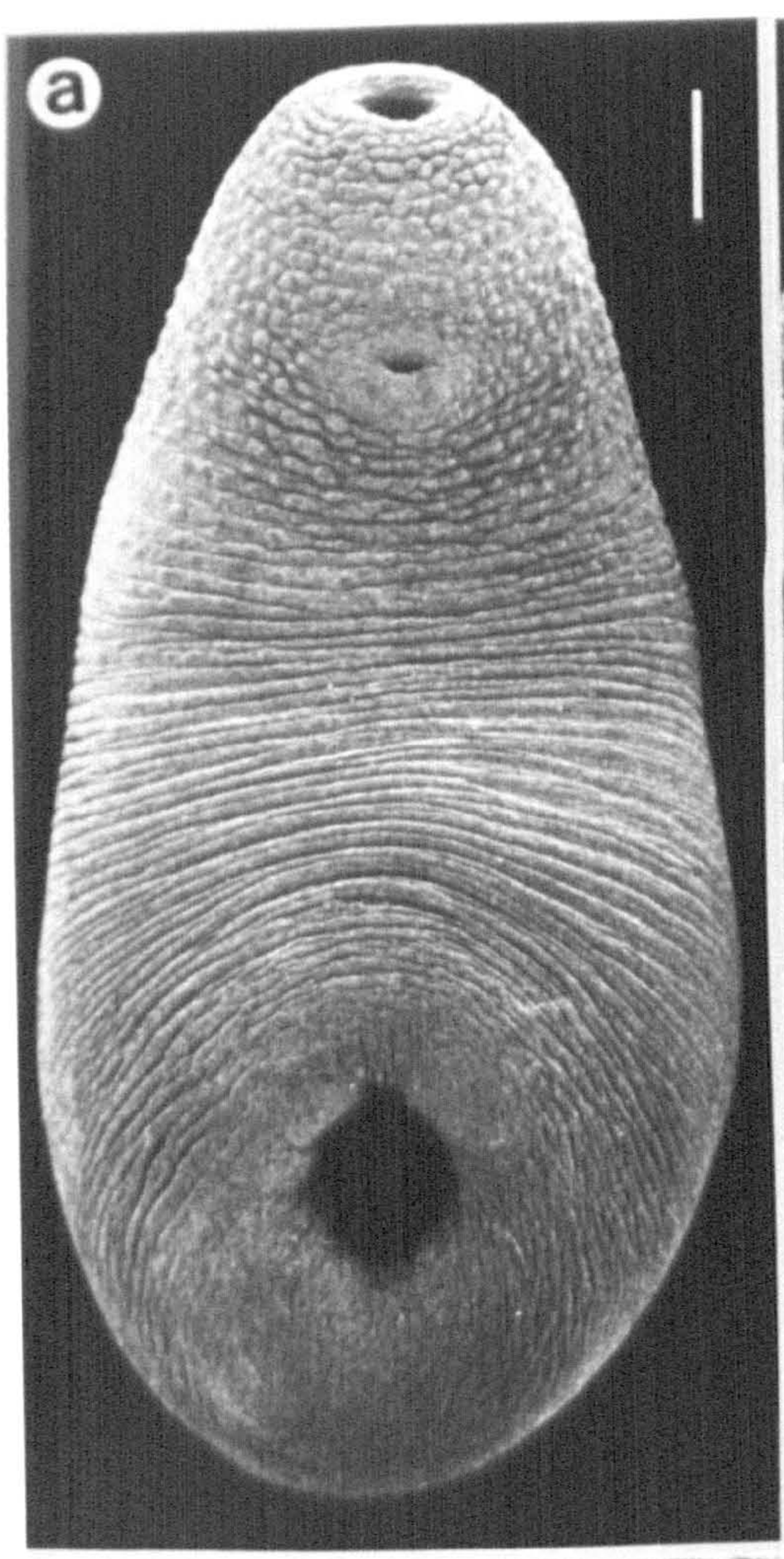
a. Whole worm, ventral view. Note large papillae on anterior half (scale bar = 300 µm)

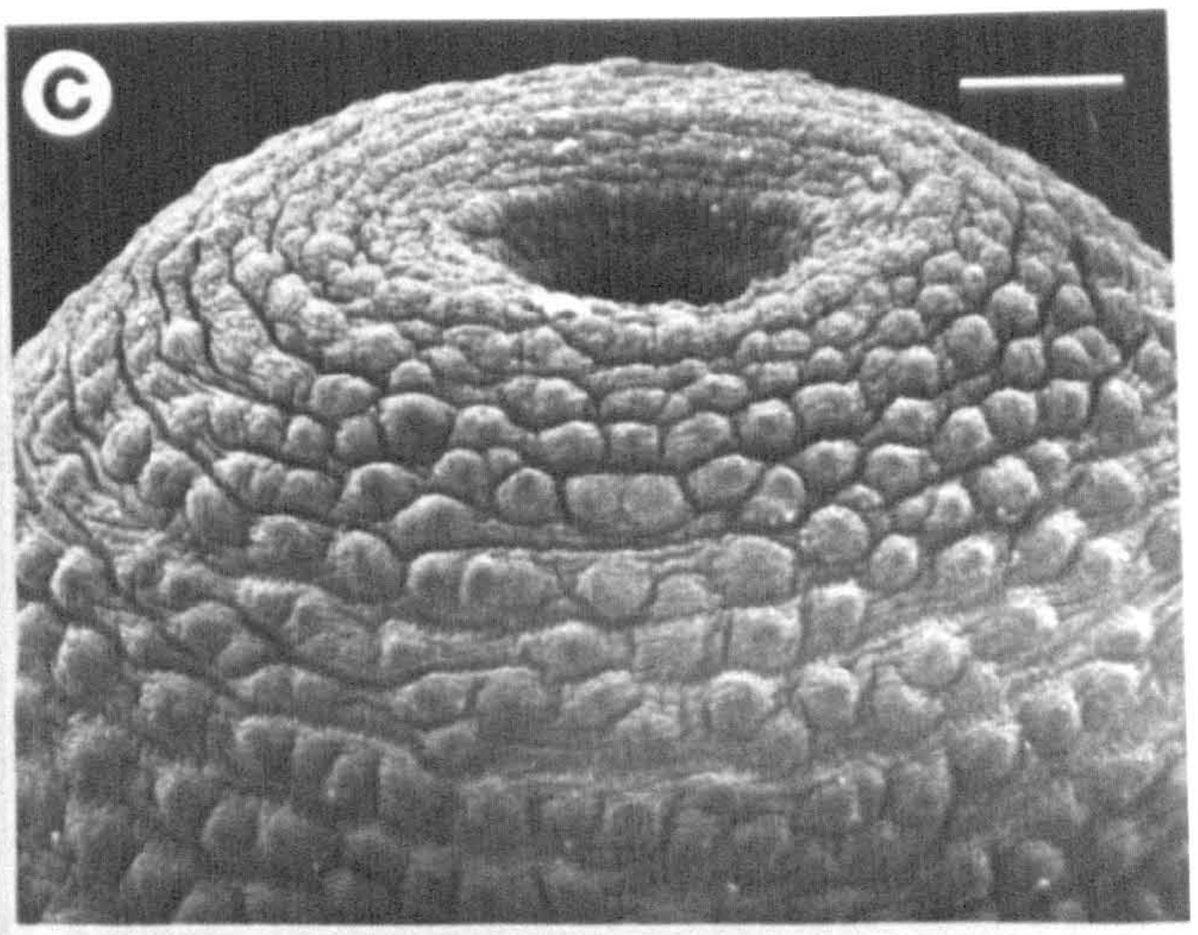
b. Acetabular region, note much smaller, fewer and randomly arranged papillae (scale bar = 200 µm)

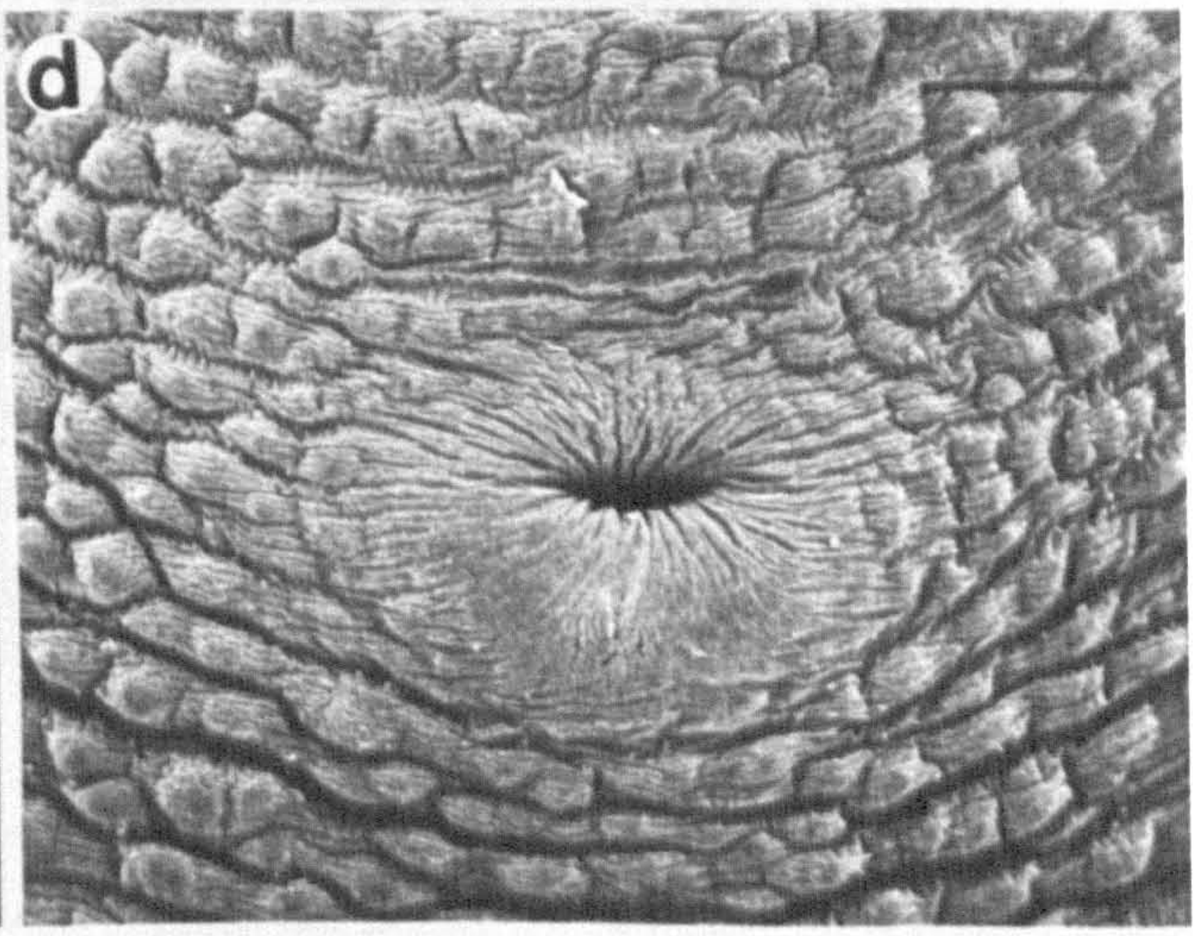
c. Anterior end showing arrangement of papillae around the oral opening (scale bar = 100 µm)

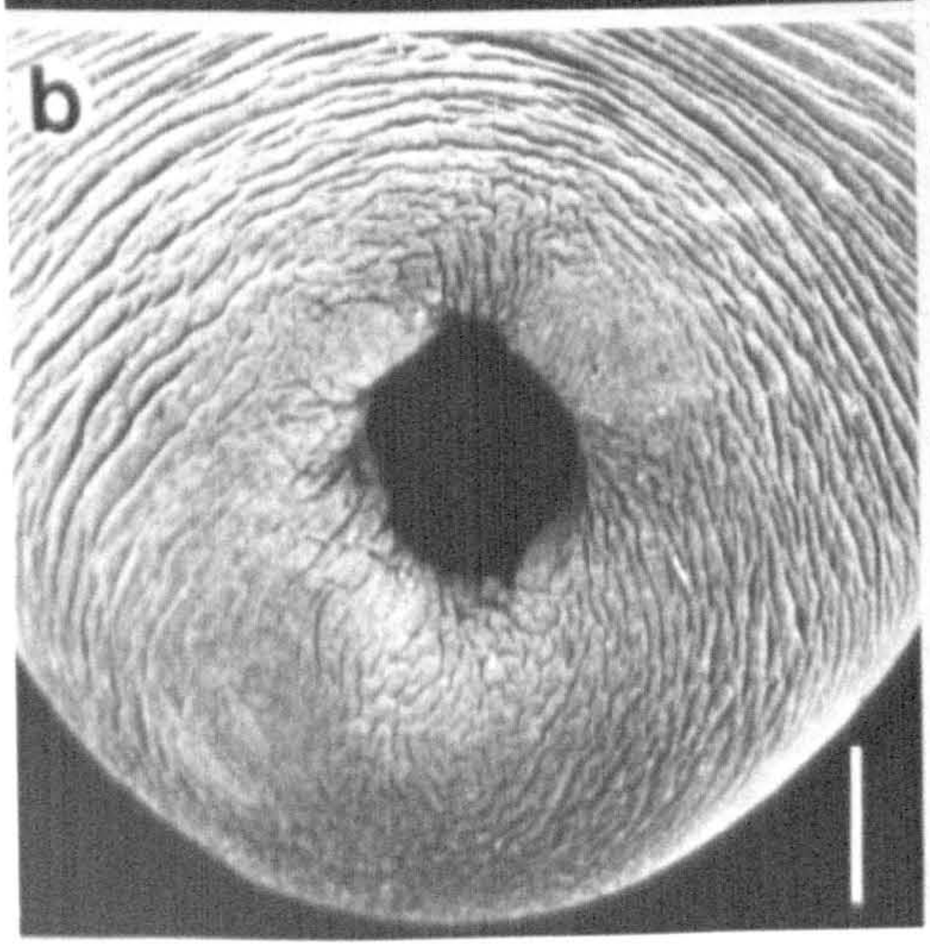
d. Genital pore region with retracted genital papilla (scale bar = 100 µm)

e. Genital pore region with everted genital papilla (scale bar = 100 µm)


a


c


d


b


e

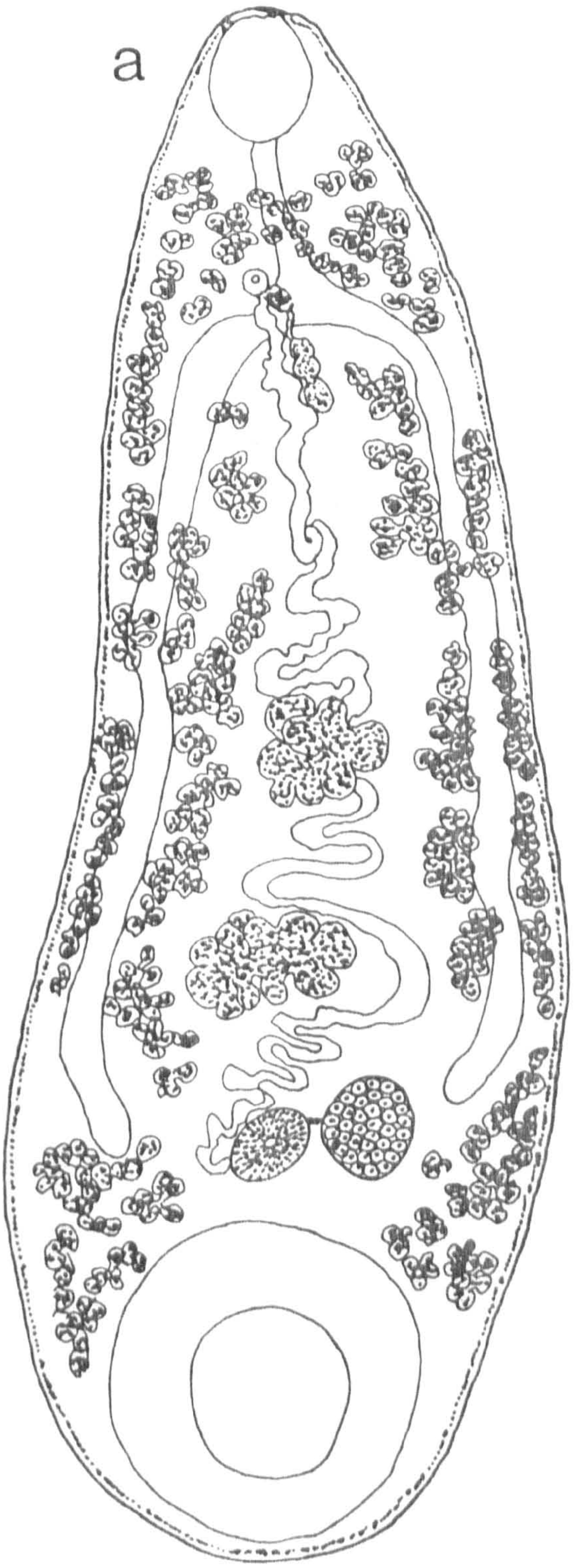
FIGURE 63

Paramphistomum hiberniae Willmott, 1950

a. Whole worm, ventral view

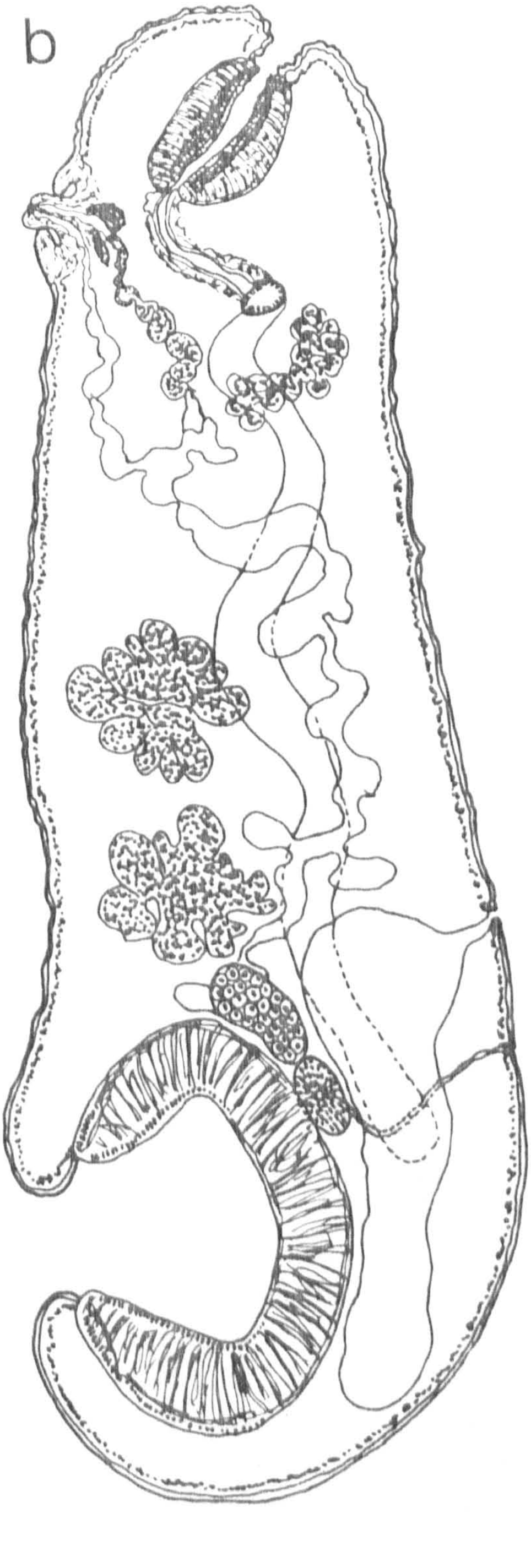
b. Whole worm, sagittal view

a



2 mm

b



1.5 mm

FIGURE 64

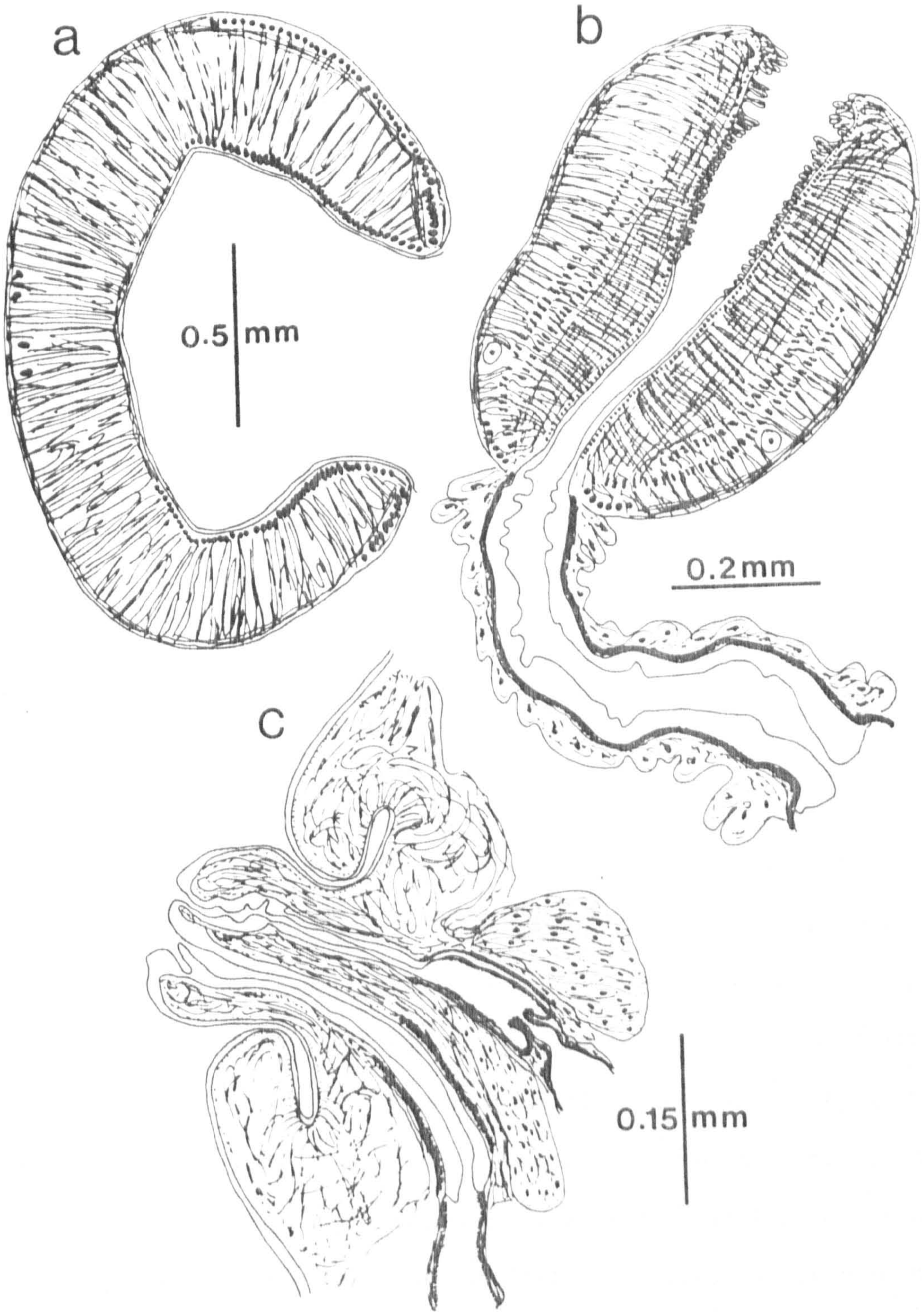
Paramphistomum hiberniae Willmott, 1950

(median sagittal section)

a. Acetabulum (paramphistomum type)

b. Pharynx (liorchis type) and oesophagus

c. Terminal genitalium (leydeni type) and pars prostatica


a
0.5 mm
b
0.2mm
C
0.15 mm

Paramphistomum cephalophi n. sp.

HOST: Cephalophus nigrifrons (black-fronted duiker)

LOCALITY: Visoke, Virungas, Rwanda (collected by R.M. Redmond)

HABITAT: Small intestine

TYPE SPECIMENS: Deposited in the helminth collection of the Commonwealth Institute of Helminthology type collection numbers S1044/A (holotype) and S1044/B (paratype).

DESCRIPTION (based on slightly immature specimens):

Body small, slender and nearly straight, 2.51-2.96 mm long; 0.72-1.25 mm in greatest width in the dorso-ventral direction; body surface lacks papillae.

Acetabulum subterminal, rim has a characteristic posterior notch, external diameter 0.70-0.78 mm in the dorso-ventral direction; ratio to body length 1:3.5 to 1:3.9; of the paramphistomum type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 13-15; d.e.c.2, 20-26; d.i.c., 30-35; v.e.c., 8-15; v.i.c., 32-37; m.e.c., 17-d0.

Pharynx 0.43-0.49 mm long, 0.33-0.35 mm wide in the dorso-ventral direction; ratio to body length 1:5.6 to 1:5.3, to the diameter of the acetabulum 1:1.4 to 1:1.6; of the cephalophi type (new type) in median sagittal section characterized by the presence of an anterior sphincter, absence of middle circular layer, weakly developed interior circular layer, exterior circular units present only in the anterior two third of the pharynx, basal circular units moderately developed, interior longitudinal fibres fairly developed, exterior longitudinal fibres very narrow and moderately developed and radial fibres moderately developed. Oesophagus 0.22-0.38 mm long, almost straight, musculature of wall thin, no bulb or

posterior sphincter; lumen lined by thin hyaline layer throughout its length. Caeca in lateral sides of the body, form seven dorso-ventral bends, reach level of acetabulum with blind ends directed ventrally.

Testes small, lobed, obliquely tandem in posterior half of the body; anterior testis 0.10-0.13 mm long, 0.14-0.15 mm in the dorso-ventral direction; posterior testis 0.12-0.14 mm long, 0.09-0.13 mm in the dorso-ventral direction; seminal vesicle slightly coiled, thin-walled and moderate in length; pars musculosa short and coiled; pars prostatica fairly developed, about three to five times longer than it is wide (0.15-0.21 by 0.04-0.06 mm).

Ovary oval, 0.12-0.15 by 0.08-0.09 mm, in between posterior testis and acetabulum; Mehlis' gland subspherical 0.08-0.09 by 0.07-0.09 mm, immediately posterior to ovary; Läurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface about 0.16-0.19 mm posteriorly to the excretory pore; uterus forms few loose coils, dorsal to testes then ventral to the male ducts; vitellaria consist of few follicles, in lateral fields, extend from level of oesophagus to anterior border of acetabulum, not confluent dorso-medially in their anterior or posterior limits, egg absent as specimens were slightly immature.

Genital pore at level of oesophageal bifurcation or immediately posterior to it; terminal genitalium of the gracile type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level of posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 65

Paramphistomum cephalophi n. sp.

(SEM)

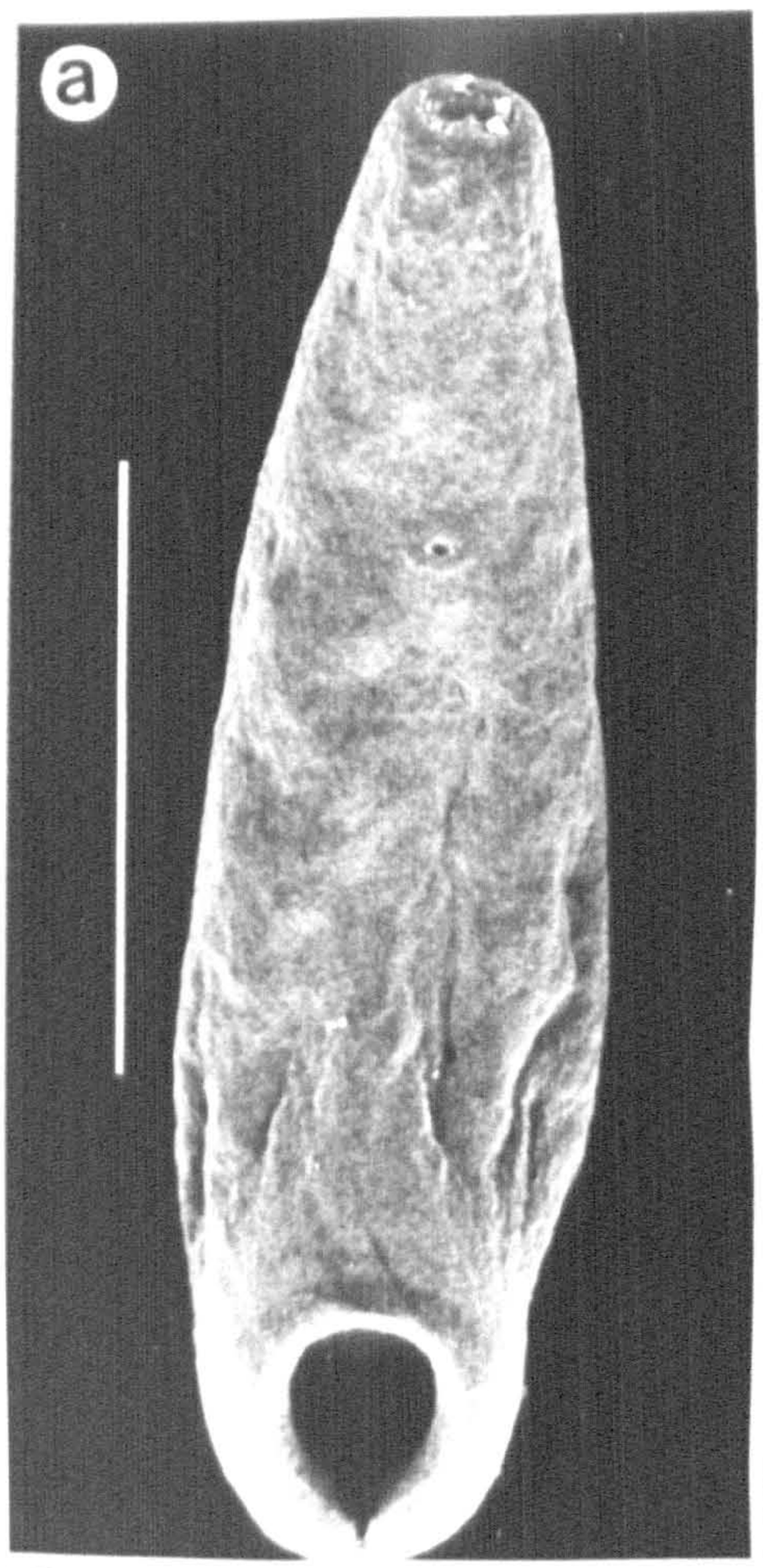
a. Whole worm, ventral view (scale bar = 1 mm)

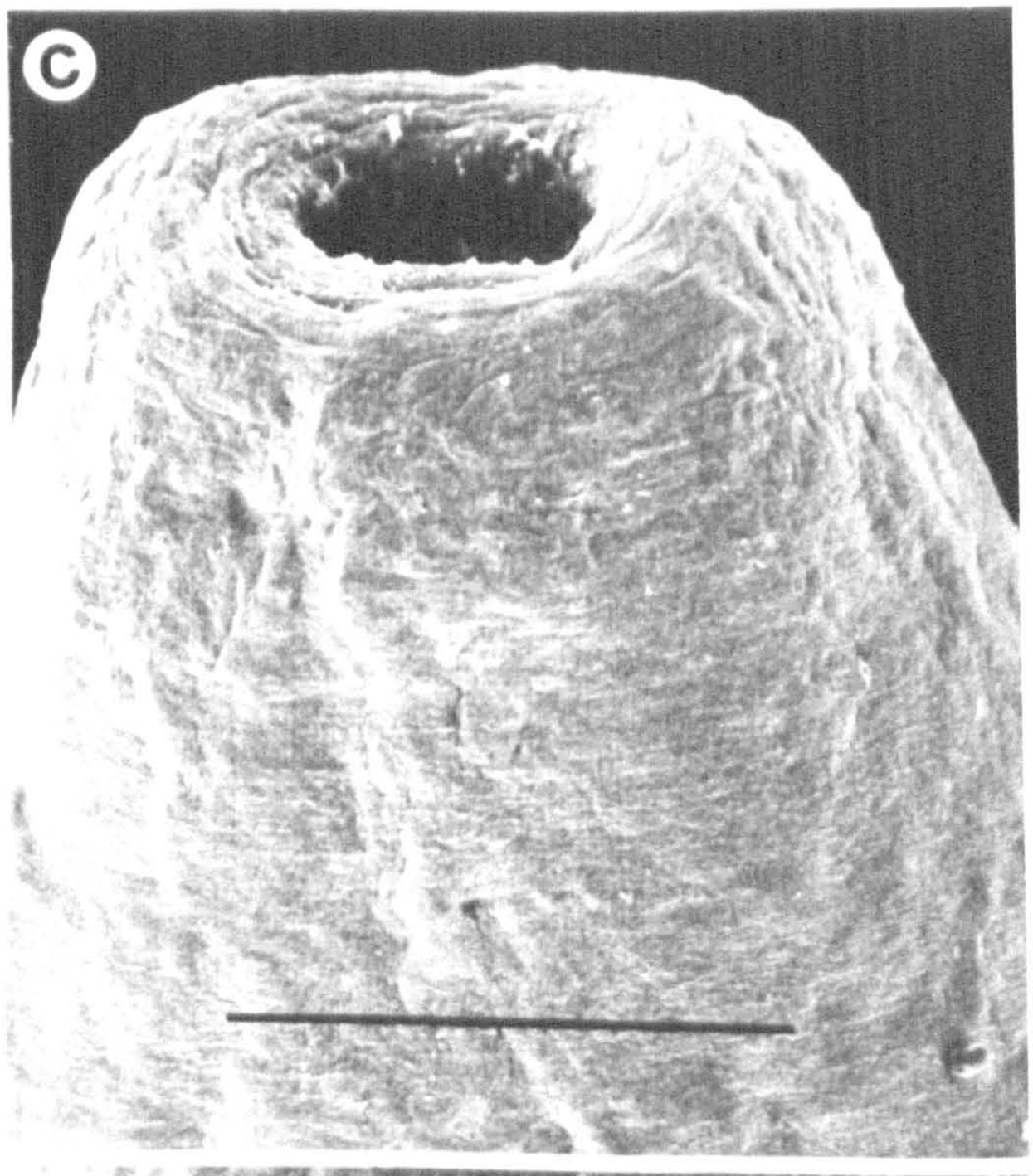
b. Genital pore region (scale bar = 20 µm)

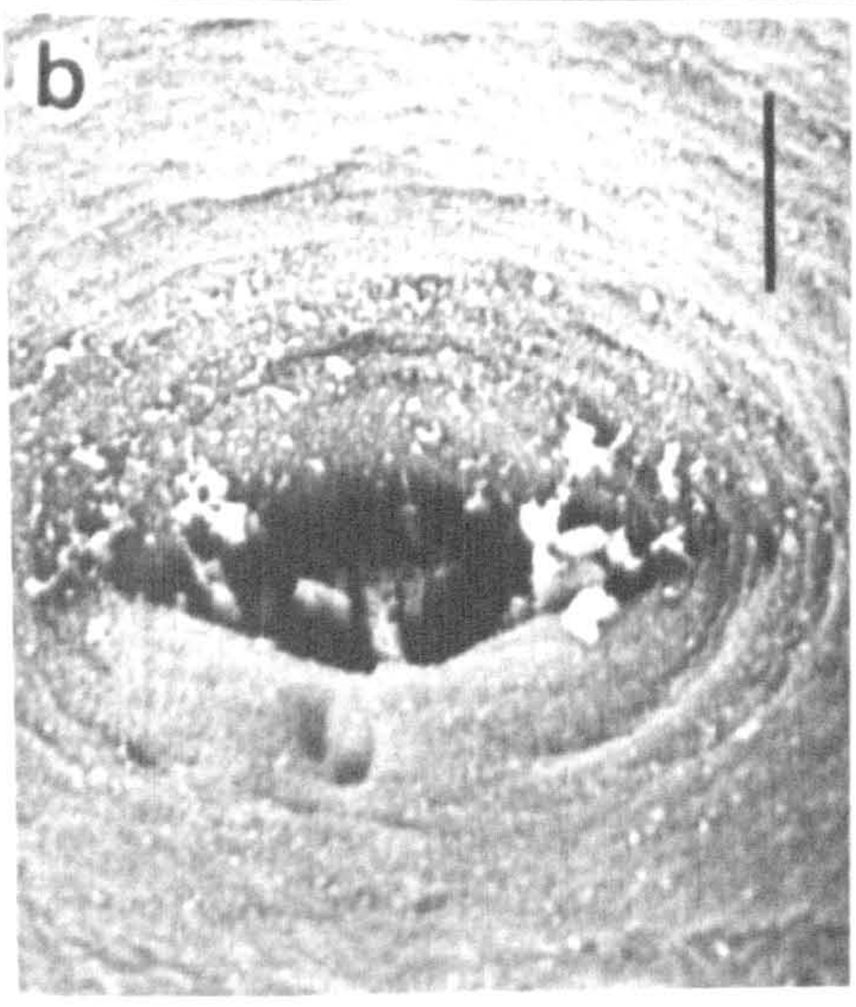
c. Anterior region (scale bar = 200 µm)

d. Acetabular region, note characteristic posterior notch (scale bar = 200 µm)

Note the absence of tegumental papillae on the surfaces.


a


c


b

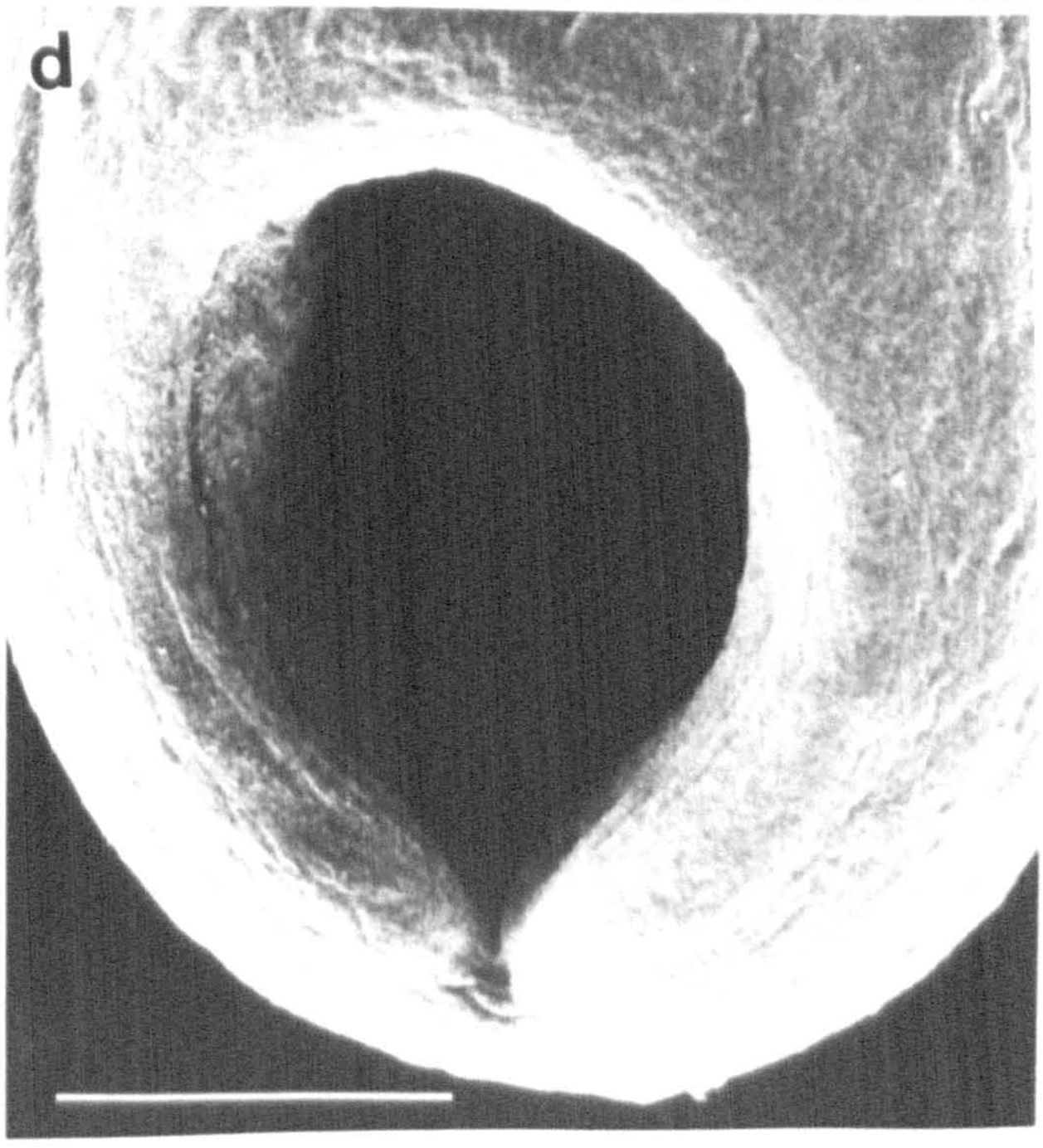

d

FIGURE 66

Paramphistomum cephalophi n. sp.

a. Whole worm, ventral view

b. Whole worm, sagittal view

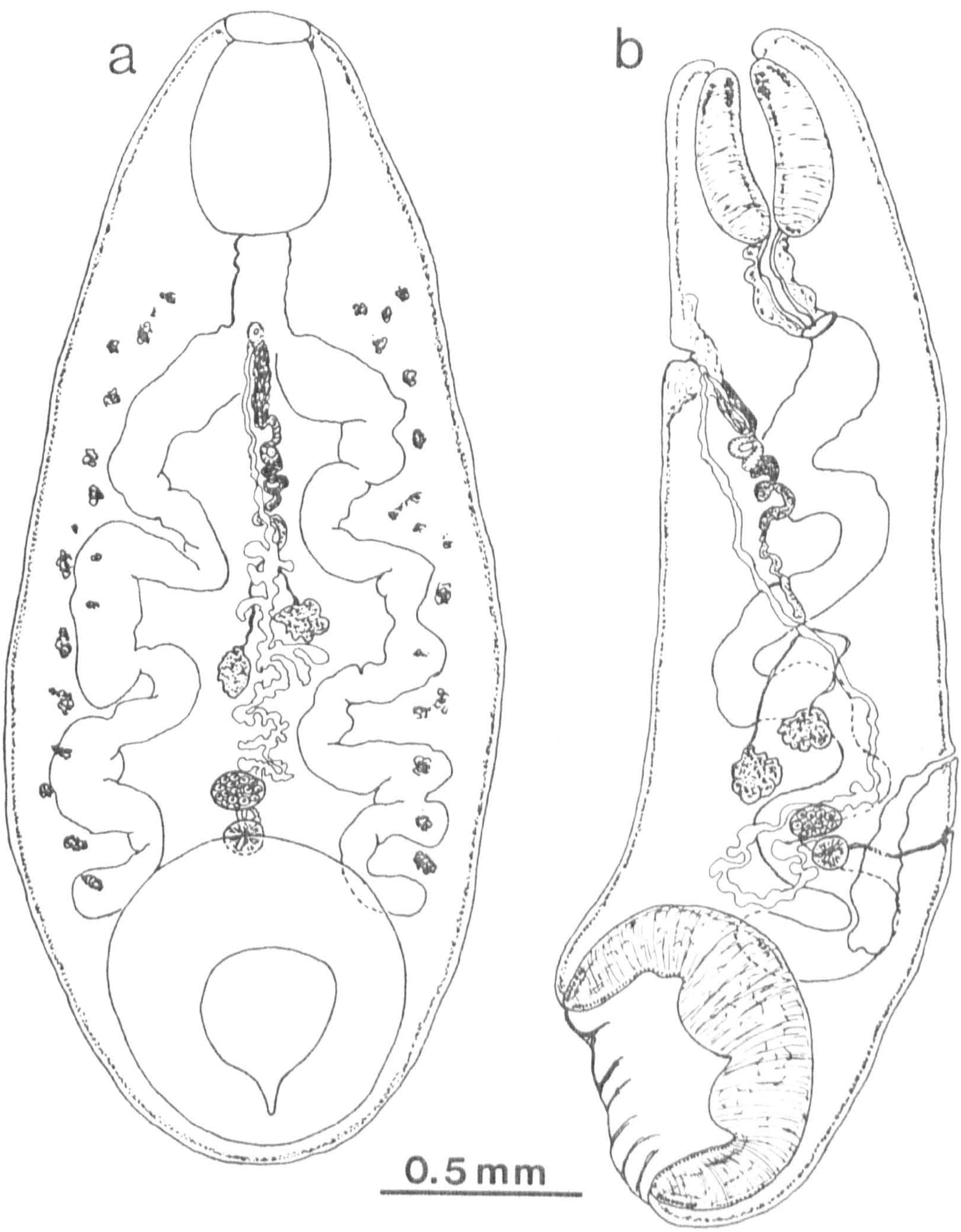

a
b
0.5 mm

FIGURE 67

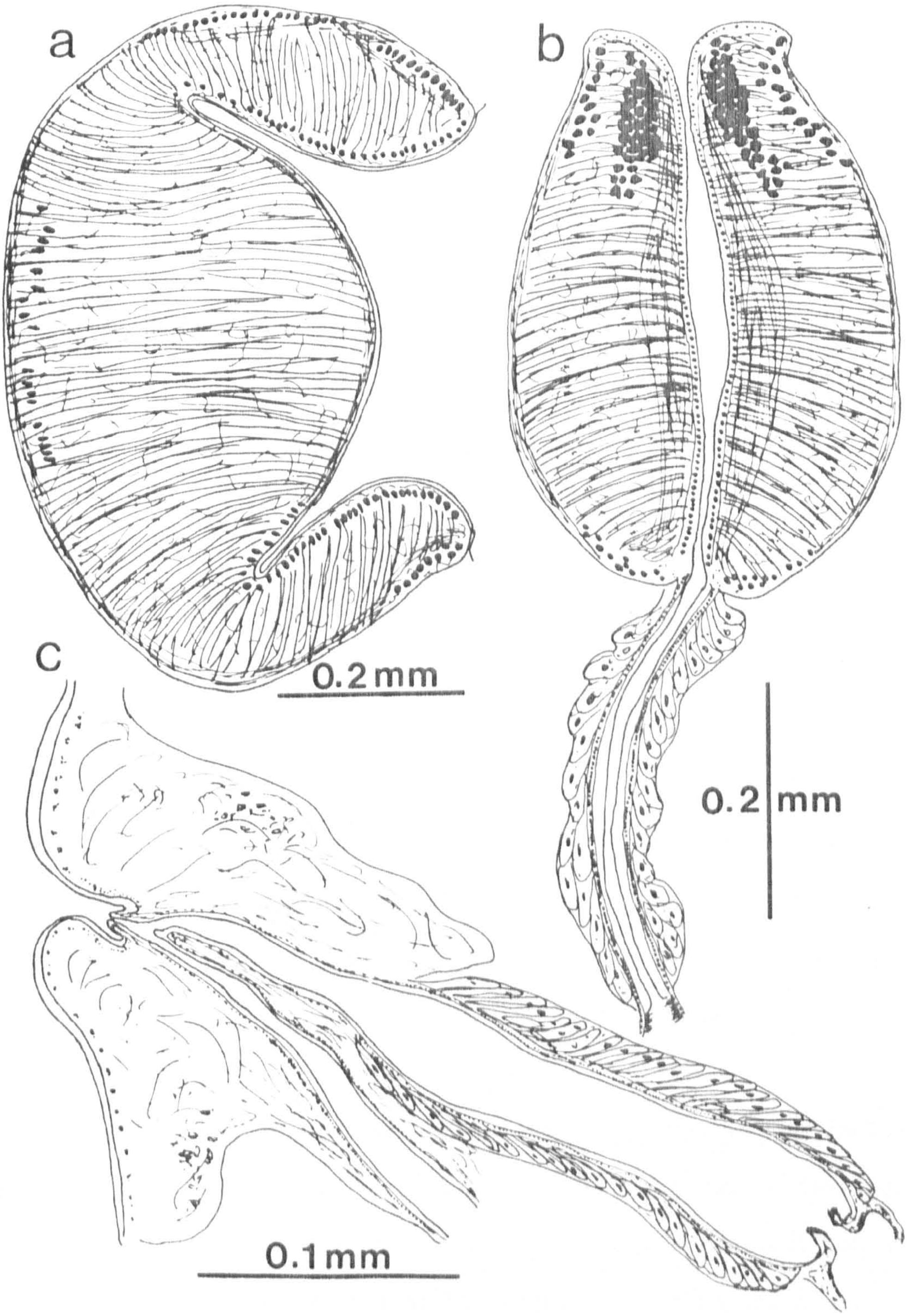
Paramphistomum cephalophi n. sp.

(median sagittal section)

a. Acetabulum (paramphistomum type)

b. Pharynx (cephalophi type) and oesophagus

c. Terminal genitalium (gracile type) and pars prostatica


a
b
0.2mm
C
0.2 mm
0.1mm

DISCUSSION

Since Fischoeder (1901) established the genus Paramphistomum for 11 species, several species have been added and the genus became a large assemblage of species. Stiles and Goldberger (1910) removed P. cotylophorum because of the presence of a genital sucker and restricted the genus to species lacking this structure. Näsmark (1937) recognised the composite nature of the genus and reduced it by removing several species and erecting new genera for their reception. The genus was further reduced when Grétillat (1958) elevated Bothriophoron Stiles and Goldberger, 1910 to full generic rank thus removing P. bothriophoron from the genus. Velichko (1966b) further reduced the number of species in the genus by establishing the genus Liorchis for P. scotiae and P. hiberniae. Yamaguti (1958, 1971) accepted Näsmark's scheme but synonymized Gigantocotyle Näsmark, 1937 with Paramphistomum and the genus once again became a large assemblage of species. However, he subdivided the genus into two subgenera, Paramphistomum (Fischoeder, 1901) and Explanatum Fukui, 1922, the latter contained the species assigned by Näsmark (1937) to the genus Gigantocotyle. Yamaguti (1971) rejected Bothriophoron either as a genus or subgenus and was unaware of the genus Liorchis since this was not included in his bibliography.

Näsmark's (1937) criteria of the genus Paramphistomum include the following: i. conical body shape; ii. Laurer's canal does not cross excretory vesicle or duct; and iii. the histological feature of the acetabulum as seen in median sagittal section which he termed "the paramphistomum type" in this genus. The first two criteria are not restricted to this genus as they are also found

in other genera. The position of Laurer's canal in relation to the excretory vesicle is now regarded as a character of value in subfamily level, differentiating the subfamily Paramphistominae (in which Laurer's canal crosses the excretory vesicle or duct) and the subfamily Orthocoeliinae (where Laurer's canal does not cross the excretory vesicle or duct). It seems that the histological feature of the acetabulum is the only character common to all species assembled by Näsmark in the genus. He has however shown that histological details of the acetabulum differ among the species he assigned under the genus Gigantocotyle. Recently described species like Paramphistomum sukari Dinnik, 1961 and Orthocoelium indonesiense Eduardo, 1980 were described to possess an acetabulum of different type from those species in the same genus. It was also observed in this study that Calicophoron raja, contrary to Näsmark's (1937) description, possesses an acetabulum different from that of Calicophoron calicophorum in that the former has a second group of circular muscle units in the dorsal exterior series which is absent in the latter. It appears therefore that the histological feature of the acetabulum like the pharynx and terminal genitalium is only of value at species level and therefore could not be used as a generic character.

The present revision does not support Näsmark's (1937) arrangement of the genus although the genera established by him as a result of splitting the genus are here recognised. For reasons given later, the genus Liorchis Velichko, 1966 is not accepted. The synonymy of Gigantocotyle Näsmark, 1937 with Paramphistomum Fischoeder, 1901 as proposed by Yamaguti (1958, 1971) and the elevation of Bothriophoron Stiles and Goldberger, 1910 to full

generic rank by Grétillat (1958) are not accepted and are discussed under the genera Gigantocotyle and Calicophoron respectively.

In the present study, it was observed that the species assigned by Näsmark (1937) to the genus Paramphistomum or the species grouped together by Yamaguti (1958, 1971) under the subgenus Paramphistomum and species recently described and assigned to the genus fall into two groups based on the development of the pars musculosa, i.e. those with short and weakly developed pars musculosa and those with long, coiled and well developed ones. The development of the pars musculosa was successfully employed in combination with other characters in separating genera in the subfamily Orthocoeliinae by Yamaguti (1971) and Eduardo (1980c). Fischoeder (1903) must have also realized its importance as a taxonomic character since he employed it in subdividing the genus into three distinct group of species. As the type of the genus, P. cervi possesses a short and weakly developed pars musculosa, it is here proposed that the genus should be restricted to those species with this kind of pars musculosa. Those species with well developed pars musculosa are similar to those species in the genus Calicophoron. Consequently therefore, P. bothriophoron (Braun, 1892); P. microbothrium Fischoeder, 1901; P. papilligerum Stiles and Goldberger, 1910; P. skrjabini Popova, 1937; P. clavula Näsmark, 1937; P. microbothrioides Price and McIntosh, 1944; P. phillerouxi Dinnik, 1961; P. sukari Dinnik, 1954; P. daubneyi Dinnik, 1962; P. sukumum Dinnik, 1964; P. petrovi (Davydova, 1961) Velichko, 1966; P. vangrembergeni Van Strydonck, 1970 and P. togolense Albaret, Bayssade-Dufour, Guilhon, Kulo and Picot, 1978 are moved to the genus Calicophoron Näsmark, 1937.

Their validity and synonymy are therefore discussed under that genus.

Velichko (1966b) erected the genus Liorchis for P. hiberniae Willmott, 1950 and P. scotiae Willmott, 1950 on the bases of the histological details of the acetabulum and pharynx only. She claimed that re-examination of the types of both species showed that their acetabula are not of the paramphistomum type as was originally described but of a new type which she termed the liorchis type and their pharynges are of a new type which she termed the pseudoliorchis type. She argued that the liorchis type of acetabulum has three groups of circular muscle units in the dorsal exterior series and two groups in the ventral exterior series with abrupt transition between each group while the paramphistomum type has only two groups of circular muscle units in the dorsal exterior series with gradual transition in size of units between each group and only a single group in the ventral exterior series. Sey (1974) however considered such differences too minor and regarded them only as variations of the paramphistomum type. Kamburov (1976) came also to the conclusion that the liorchis type of acetabulum and pseudoliorchis type of pharynx are in fact variations of the paramphistomum and liorchis types respectively and therefore the genus Liorchis is synonymous with Paramphistomum. Kotrlá and Chroust (1978) and Odening, Bockhardt and Gräfner (1978) also expressed the view that Liorchis is not a valid genus.

The writer has re-examined the types of P. hiberniae and P. scotiae (L.S.H.T.M. type collection numbers 332-338, 331 and 340-346 respectively) and confirms Willmott's (1950b) original description that their acetabula and pharynges are of the paramphistomum and liorchis types respectively. What was regarded

by Velichko as the middle or second group of circular units in the dorsal exterior series of the acetabulum is actually the inner half of the first group. Although the units in this half are slightly smaller in size than those in the outer half, they are not separated from the latter by a band of oblique muscle fibres, hence can only be regarded as one group. In fact, the dorsal exterior series is divided only into two groups of units by a band of oblique muscle fibres and not into three groups as claimed by Velichko. The ventral exterior series as was originally described, consists only of a single group of units and not of two groups as claimed by Velichko. The pharynx of both species is of the liorchis type, as was originally described and the reasones given by Velichko in establishing the pseudoliorchis type of pharynx are unfounded. In view of the above, the writer agrees with Sey (1974), Kamburov (1976), Kotrlá and Chroust (1978) and Odening, Bockhardt and Gräfner (1978) that the genus Liorchis is synonymous with Paramphistomum.

The genus Srivastavaia was established by Singh (1970) for a single species, S. indica recovered from esperimentally infected sheep and goats with metacercariae from naturally infected Indoplanorbis exustus in India. Although the description on general morphology was based on several flattened specimens, observations made on the details of the acetabulum, pharynx and terminal genitalium and the relationship between Laurer's canal and the excretory vesicle were based only on a single specimen sagittally sectioned for this purpose. The species was also described to closely resemble P. thapari Price and McIntosh, 1953 (= Cotylophoron indicum Stiles and Goldberger, 1910) which is regarded here as a junior synonym of P. epiclitum Fischoeder, 1904. The type specimens of Srivastavaia

indica loaned from the British Museum (Natural History) were re-examined and found to be identical in all respects with P. epiclitum. What was described by Singh (1970) as streptocoelium type of acetabulum is actually of the paramphistomum type because the dorsal exterior circular series is divided into two groups of units and all other details agree with the latter type. Contrary to the original description, Laurer's canal crosses the excretory vesicle at its posterior half. What was described as genital sucker is not a true one but of the same kind found in P. epiclitum, consequently the genus Srivastavaia becomes a synonym of Paramphistomum.

Stiles and Goldberger (1910) described Cotylophoron indicum as new species from Ovis aries in India. Price and McIntosh (1953) re-examined the type specimens and found that the dorsal exterior circular series in the acetabulum is divided into two groups of units. They consequently moved the species to the genus Paramphistomum and as there is already a species in the genus of that name, they gave the name Paramphistomum thapari for it. The writer has also re-examined the type specimens of Cotylophoron indicum loaned from the United States National Parasite Collection (USNMH Coll. No. 5781) and confirms Price and McIntosh's observation of the histology of its acetabulum. However, the species is identical in all respects with specimens of P. epiclitum examined in this study. What was described by Stiles and Goldberger (1910) as genital sucker is not a true one since the wall of the terminal genitalium of this species does not conform to the genital sucker musculature as in the cotylophoron type of terminal genitalium.

Because of the semi-circular appearance of the wall of the terminal genitalium, it gives a false impression of a sucker.

Paramphistomum indicum was described by Stiles and Goldberger (1910) from the zebu (Bos indicus) in the Punjab, India and was reported to be closely related to P. gracile. Maplestone (1923), without re-examining the type specimens, regarded it as a synonym of P. cervi, a view followed by Travassos (1934) and Dawes (1936). Skrjabin (1949) regarded it synonymous with Cotylophoron indicum. The type specimens of this species loaned from the United States National Parasite Collection (USNMH Coll. No. 1732) were carefully re-examined. These consisted of the original sections made by Stiles and Goldberger (1910) and additional sections made later and labeled "P. gracile" by McIntosh (according to Dr. Lichtenfels, this identification is unpublished) from the original unsectioned materials of Stiles and Goldberger. It was observed in this study that the original sections of Stiles and Goldberger are identical in all respects with P. gracile while the sections made by McIntosh are identical with P. epiclitum. It is apparent that Stiles and Goldberger were dealing with two species. This is also shown in their illustrations; Fig. 92 and 93 show tegumental papillae whose distribution is similar to that found in specimens of P. epiclitum examined in this study and Fig. 94 and 95 show internal details conforming to the internal morphology of P. gracile. Paramphistomum indicum is therefore regarded here as synonyms in part of P. gracile and in part of P. epiclitum.

Paramphistomum malayi was described by Lee and Lowe (1971) as a new species from Bubalus bubalis in Malaysia. The terminal

genitalium was described to resemble that of Cotylophoron cotylophorum but not identical with it because of its smaller size and weaker musculature which is arranged differently. Only one paratype of the species was available for re-examination loaned by the senior author and according to her (personal communication), the rest of the types were lost. Re-examination of this paratype revealed without doubt that the species is identical with P. epiclitum and is therefore regarded here as a junior synonym of the latter.

Gupta (1958a) described Cotylophoron madrasense from sheep in Madras, India. Gupta and Gupta (1972b) described Cotylophoron chauhani from sheep in Ernakulam, India. Both species closely resemble each other except that the latter was described to possess an oesophageal sphincter and testes which are arranged diagonally. From the authors' illustration of C. chauhani, the oesophagus (Fig.4) does not show a distinct sphincter but rather only a slight thickening of the oesophageal wall at its junction with the caeca and the testes (Fig. 1) are not widely diagonal but only slightly oblique and tandem as in C. madrasense. Both species are therefore regarded as one and the same species. In both species, no deposition of the type specimens was indicated and efforts to obtain the types and other specimens from the authors have failed despite several letters. From the authors' descriptions and illustrations however, both species are identical with P. epiclitum. Cotylophoron madrasense and C. chauhani therefore are regarded here as junior synonyms of P. epiclitum.

Paramphistomum julimarinorum and P. nicabrasilorum were described by Velazquez-Maldonado (1976) from Bos taurus in Brazil. Both species were separated from each other only by slight differences in the length of the pharynx and its internal papillae distribution and the length of the excretory canal. These characters are often subject to variations depending on the state of the worm during fixation, hence both species can only be regarded as one and the same species. Several requests were made for the loan of the type specimens, both from the author and from the head of the department where these are supposed to have been deposited, but without success. From the author's own descriptions and illustrations, both species are identical with P. leydeni and therefore are regarded here as synonyms of the latter.

Paramphistomum bombayiensis was described by Gupta and Verma (in Gupta and Nakhasi, 1977a) as new species from Bos indicus and Bubalus bubalis in India. The description was very brief and accompanied by a note that the species is under publication, but no further detailed description has appeared yet. Repeated requests for the loan of the type specimens from the authors were met with silence. From their own description and illustration, the species is identical in all respects with P. gracile. What was mentioned as the bombayiensis type of terminal genitalium (Fig. 12) conforms with the gracile type as described by Näsmark (1937). The species therefore falls as a junior synonym of P. gracile.

Paramphistomum spinecephalus was described by Tandon (1955a) from Bubalus bubalis in India and moved by Mukherjee (1960) as cited in and accepted by Mukherjee and Chauhan (1965) to the genus

Ceylonocotyle Näsmark, 1937 which is now a junior synonym of Orthocoelium (Stiles and Goldberger, 1910). Yamaguti (1971) retained the species in the genus Paramphistomum but with a note "generic status sub judice". The type specimens could not be traced but it is clear from the author's own description and illustration that the species in question belongs to the genus Orthocoelium and its specific status is discussed under that genus.

Schad, Kuntz, Anteson and Webster (1964) renamed Paramphistomum gotoi of Dawes (1936) and of Tandon (1955b) as Ceylonocotyle gigantopharynx because they found out that the species is not identical with P. gotoi Fukui, 1922 by examining several specimens from Bubalus bubalis in Borneo, Malaysia. Yamaguti (1958, 1971) accepted its validity but listed the species under the genus Paramphistomum without giving any reason. The writer has re-examined the original material of Dawes (1936) identified as P. gotoi deposited in the British Museum (Natural History) and found out that it is not identical with P. gotoi Fukui, 1922 but agrees with Ceylonocotyle gigantopharynx Schad, Kuntz, Anteson and Webster, 1964. Materials of this species from Bos taurus and Bubalus bubalis in the Philippines were also examined. The species is characterized by Laurer's canal which does not cross the excretory vesicle or duct and the well developed pars musculosa, features common to all species of the genus Orthocoelium. Schad et al (1964) were right in assigning the species to the genus Ceylonocotyle but since this genus is now a synonym of Orthocoelium, the species becomes Orthocoelium gigantopharynx (Schad, Kuntz, Anteson and Webster, 1964) n. comb. and is described and discussed in detail under this genus.

The validity of P. leydeni, P. hiberniae and P. scotiae has been questioned by several workers. Velichko (1966b) regarded P. hiberniae and P. scotiae as separate species under the genus Liorchis but later (1971) considered both as one and the same species. Sey (1974) expressed the view that morphologically, P. scotiae is either very closely related to or identical with P. leydeni. Kotrla and Choust (1978) also regarded P. scotiae synonymous with P. leydeni. Kamburov (1976) regarded P. hiberniae and P. scotiae both as synonyms of P. cervi while Odening, Bockhardt and Gräfner (1978) considered both species and P. leydeni all synonyms of P. cervi.

P. leydeni is a distinct species, it is easily distinguished from P. cervi by the presence of tegumental papillae on the body surface and the different type of terminal genitalium. P. hiberniae was also found to be a distinct and valid species. Like P. leydeni, it differs from P. cervi by the presence of tegumental papillae and the different type of terminal genitalium. However, it is distinguished from P. leydeni as well as from P. cervi by the vitellaria being confluent dorso-medially in their anterior limit. P. scotiae on the other hand was found to be identical with P. leydeni after a re-examination of its type specimens thus confirming the view earlier expressed by Sey (1974).

Davydova-Velichko (1964) has shown that the species, Cotylophoron vigisi which she described as new (Davydova, 1963) is in fact Paramphistomum ichikawai Fukui, 1922 after a careful re-examination of the type specimens and examination of new materials, thus the former name falls as a junior synonym of the latter. Paramphistomum procapri was described by Wang (1979)

as new species from Procapra picticaudata in China. The species was differentiated from P. leydeni only by slight differences in the ratio of acetabulum and pharynx to the body length, a character which is unstable owing to the variability of the body length as affected by several factors already mentioned earlier in this work. The species in question therefore is considered here a junior synonym of P. leydeni.

Evans and Rennie (1908) briefly described and illustrated but without specific identification two amphistomes, one from the caecum and the other from the biliary duct of ox in Burma. Railliet (1924) gave the names, Paramphistomum microon and P. birmense respectively but without re-examination of the original materials. Dawes (1936) regarded both species as synonyms of P. cervi or P. explanatum. Näsmark (1937) without having any material for examination transfered P. birmense to the genus Gigantocotyle because of its biliary location and P. microon to the genus Calicophoron because Railliet (1924) previously assigned it to the same group as P. calicophorum. Hsu (1935) reported with brief description Paramphistomum chinensis as new species from a cow in Soochow, China. Yamaguti (1958, 1971) regarded it as a synonym of Orthocoelium orthocoelium (Fischoeder, 1901) Price and McIntosh, 1953. Wang (1979) described Paramphistomum pseudocuonum as new species from Canis familiaris in China. The description was based on only two pressed specimens thus the structures of the pharynx, acetabulum and terminal genitalium were not observed. The type specimens of the above mentioned species could not be traced. From the very brief description and inadequate illustration available, it is very difficult to determine their generic position

and to verify their specific identity. Until new materials are made available for redescription, the above species are regarded here species inquirendae.

When Näsmark (1937) classified the terminal genitalia of paramphistomids into different types based on available materials at that time, he referred the terminal genitalium of P. epiclitum and P. leydeni to the same type, i.e. the epiclitum type. However, re-examination of Näsmark's materials and examination of several specimens from various hosts and localities of both species revealed that their terminal genitalia differ, that of P. epiclitum as rightly defined by Näsmark, is semi-circular in outline while that of P. leydeni is not but of a different form. Because of this, one is easily distinguished from the other. It is here proposed that the epiclitum type as defined by Näsmark (1937) be retained but only for P. epiclitum and a new type, the leydeni type for P. leydeni. This type is already defined earlier in this work. Willmott (1950b) referred the terminal genitalium of P. hiberniae to the ichikawai type but re-examination of the type specimens revealed that it is not of that type but of the leydeni type.

Only the following species are retained and considered valid under the genus: Paramphistomum cervi (Zeder, 1790) Fischoeder, 1901 (type species); P. liorchis Fischoeder, 1901; P. gracile Fischoeder, 1901; P. epiclitum Fischoeder, 1904; P. gotoi Fukui, 1922; P. ichikawai Fukui, 1922; P. leydeni Näsmark, 1937 and P. hiberniae Willmott, 1950. A new species, Paramphistomum cephalophi is described and illustrated from the black-fronted duiker (Cephalophus nigrifrons) in Rwanda. It is assigned to the

genus Paramphistomum because Laurer's canal crosses the excretory vesicle or duct, the acetabulum is of moderate size, there is no pharyngeal pouch or diverticle, no ventral pouch, no genital sucker and the pars musculosa is short and weakly developed. It differs from other species of the genus in the presence of an anterior sphincter in the pharynx and the characteristic posterior notch of the acetabular rim. A key to the species of the genus is given below.

Cotylophoron indicum Stiles and Goldberger, 1910 (= Paramphistomum thapari Price and McIntosh, 1953); C. madrasense Gupta, 1958; C. chauhani Gupta and Gupta, 1972; Paramphistomum indicum Stiles and Goldberger, 1910 in part; P. malayi Lee and Lowe, 1971 and Srivastavaia indica Singh, 1970 are all considered synonyms of Paramphistomum epiclitum Fischoeder, 1904. Consequently, the genus Srivastavaia Singh, 1970 becomes a synonym of Paramphistomum Fischoeder, 1901. The genus Liorchis Velichko, 1966 is also regarded as a synonym of Paramphistomum.

Paramphistomum indicum Stiles and Goldberger, 1910 in part and P. bombayiensis Gupta and Verma in Gupta and Nakhasi, 1977 are regarded as synonyms of Paramphistomum gracile Fischoeder, 1901 and Cotylophoron vigisi Davydova, 1963 is considered synonymous with Paramphistomum ichikawai Fukui, 1922.

Paramphistomum julimarinorum Velazquez-Maldonado, 1976; P. nicabrasilorum Velazquez-Maldonado, 1976; P. procapri Wang, 1979 and Cotylophoron skrjabini Mitskevich, 1958 are all regarded as synonyms of Paramphistomum leydeni Näsmark, 1937. The synonymy of Paramphistomum scotiae Willmott, 1950 with P. leydeni Näsmark,

1937 as previously suggested by Sey (1974) and Kotrla and Chroust (1978) is confirmed.

Paramphistomum birmense Railliet, 1924; P. microon Railliet, 1924; P. chinensis Hsu, 1935 and P. pseudocuonum Wang, 1979 are considered species inquirendae.

Key to the species of the genus Paramphistomum Fischoeder, 1901

1. Pharynx with anterior sphincter, of the cephalophi type; acetabular rim with posterior notch- - P. cephalophi n. sp.

   Pharynx without anterior sphincter; acetabular rim without posterior notch - - - - - - - - - - - - - - - - - - 2

2. Vitellaria confluent dorso-medially in their anterior limit- - 3

   Vitellaria not confluent dorso-medially - - - - - - - - - - - 4

3. Pharynx of the liorchis type; terminal genitalium of the leydeni type - - - - - - - - - - - - - - - - - - - P. hiberniae

   Pharynx of the calicophoron type; terminal genitalium of the ichikawai type - - - - - - - - - - - - - - - - - P. ichikawai

4. Testes lobed - 5

   Testes not lobed - - - - - - - - - - - - - - - - - - - P. liorchis

5. Pharynx of the liorchis type - - - - - - - - - - - - - - - - - 6

   Pharynx of the calicophoron type - - - - - - - - - - - - - - - 8

6. Blind caecal ends usually meet dorso-medially; terminal genitalium of the gracile type - - - - - - - - - - - P. gotoi

   Blind caecal ends do not meet dorso-medially - - - - - - - - - 7

7. Body surface lacks tegumental papillae; terminal genitalium of the gracile type - - - - - - - - - - - - - - - - P. cervi

   Body surface has tegumental papillae; terminal genitalium of the leydeni type - - - - - - - - - - - - - - - - - P. leydeni

8. Terminal genitalium of the epiclitum type; tegumental papillae extensive, present on around oral opening and anterior ventral half of the body - - - - - - - - - - - - P. epiclitum

   Terminal genitalium of the gracile type; tegumental papillae present only on around the oral opening - - - - P. gracile

Revision of the genus Calicophoron Näsmark, 1937

INTRODUCTION

Näsmark (1937) in his revision of the family Paramphistomidae Fischoeder, 1901 established the genus Calicophoron after examining materials of Paramphistomum calicophorum Fischoeder, 1901 and P. ijimai Fukui, 1922 and transfered them to his genus in new combinations. By tautonomy, the former is the type species of the genus. He described Calicophoron raja as new species from cattle in the Sudan. Although he had no materials for examination of Paramphistomum crassum Stiles and Goldberger, 1910; P. cauliorchis Stiles and Goldberger, 1910; P. papillosum Stiles and Goldberger, 1910 and P. microon Railliet, 1924, he moved them to his new genus in new combinations.

With the exception of Lee and Lowe (1971), subsequent authors including Skrjabin (1949), Yamaguti (1939, 1958, 1971), Durie (1951), Swart (1954) Gupta (1965b), Gupta and Gupta (1972a) and Velichko (1973) accepted the genus. New species have been recently described under the genus namely: C. erschovi Davydova, 1959 from cattle in Azerbaidzhan, USSR; C. orientalis Mukherjee, 1966 from sheep in India and C. wuchengense Wang, 1979 and C. zhejiangense Wang, 1979 both from Bubalus bubalis in China.

In the present study, types whenever available and additional materials of as many species as possible were critically examined. As a result, the genus Calicophoron Näsmark, 1937 is upheld but redefined. As a consequence, some species previously described

under the genus Paramphistomum Fischoeder, 1901 are transfered to the genus in new combinations. The valid species are here redescribed and illustrated and the synonymy of the other species is discussed.

SYNONYM: Bothriophoron (Stiles and Goldberger, 1910) Grétillat, 1958

GENERIC DIAGNOSIS

Paramphistomidae, Paramphistominae. Body conical, broader posteriorly than anteriorly, almost round in cross section; ventral pouch absent. Acetabulum subterminal, not enormous but moderate in size. Pharynx without pouch or diverticle; oesophagus with or without posterior sphincter or bulb; caeca in lateral sides of the body, usually sinuous in their course. Testes lobate, directly or obliquely tandem or side by side; seminal vesicle thin-walled and strongly coiled; pars musculosa thick-walled, well developed and convoluted; pars prostatica moderately to well developed; cirrus pouch absent. Ovary and Mehlis' gland posttesticular; uterus winds forward, dorsal to the testes then ventral to the male ducts; Laurer's canal crosses the excretory vesicle or duct; vitellaria in lateral fields, may or may not be confluent dorso-medially. Genital sucker absent. Parasitic in the stomach of ruminants.

Type species: Calicophoron calicophorum (Fischoeder, 1901) Näsmark, 1937

Calicophoron calicophorum (Fischoeder, 1901) Näsmark, 1937

Synonyms: Paramphistomum crassum Stiles and Goldberger, 1910
Paramphistomum cauliorchis Stiles and Goldberger, 1910
Paramphistomum ijimai Fukui, 1922
Paramphistomum (Cauliorchis) skrjabini Popova, 1937
Paramphistomum erschovi Davydova, 1959
Calicophoron orientalis Mukherjee, 1966
Calicophoron wuchengense Wang, 1979
Cotylophoron skrjabini Mitskevich, 1958 in part

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collections

Axis axis	India	British Museum (Natural History) coll. no. 1965 4.2.31-45, labeled "P. cauliorchis".
Bos taurus	Australia	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Korea	Dr. Du-Hwan Jang
	New Zealand	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Bos indicus	Burma	British Museum (Natural History) coll. no. 1957. 12.30.281-300.
	Malaysia	British Museum (Natural History) coll. no. 1966. 2.17.1 & 1965.1.27.7-8.
	Sri Lanka	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.

Bos indicus	Vietnam	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Cattle	Australia	Dr. J. C. Boray
		British Museum (Natural History) coll. no. 1950.12. 6.90-100.
	Fiji	Commonwealth Institute of Helminthology
	Hong Kong	British Museum (Natural History) coll. no. 1928. 9.28.63-68.
	Solomon Islands	British Museum (Natural History) coll. no. 1191/78
	Sri Lanka	Dr. Sheila Willmott
	Thailand	London School of Hygiene & Tropical Medicine
Bubalus bubalis	India	London School of Hygiene & Tropical Medicine coll. no. 640.
		Commonwealth Institute of Helminthology, Dr. J.A. Dinnik's collection, labeled "C. cauliorchis".
	Urimo, Papua New	British Museum (Natural History) coll. no. 325/7
Capra hircus	Fiji	Commonwealth Institute of Helminthology
	Korea	Dr. Du-Hwan Jang
	Taiwan	Prof. Yung-Chi Lee

Capra hircus	Vietnam	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
sheep	Australia	Dr. J. C. Boray

HABITAT: Rumen and reticulum

DESCRIPTION:

Body pear-shaped, may bend slightly ventrally, decidedly broader at the acetabular region, 8.00-15.30 mm long, 3.60-7.50 mm in the dorso-ventral direction. Body surface has large dome-shaped papillae densely arranged around oral opening and from this point ventrally to about the middle of the body except an oval area surrounded by a ridge around the genital pore region which is free of papillae. Much smaller papillae are also found randomly arranged around the acetabular opening.

Acetabulum subterminal, external diameter 1.60-3.20 mm in the dorso-ventral direction; ratio to body length 1:2.6 to 1:6.2; of the calicophoron type (sensu Näsmark, 1937) in median sagittal section; number of circular muscule units, d.e.c., 12-23; d.i.c., 36-46; v.e.c., 39-54; v.i.c., 12-25; m.e.c., 10-18.

Pharynx 0.72-1.95 mm long, 0.60-1.36 mm in the dorso-ventral direction; ratio to body length 1:5.6 to 1:10.7, to the diameter of the acetabulum 1:1.3 to 1:2.1; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section; internal surface lined by small dome-shaped papillae. Oesophagus 0.58-1.51 mm long, may be straight, or may bend dorsally depending on the state of relaxation of the worm, musculature of wall more or less uniform in thickness, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of

the body, form irregular dorso-ventral bends, reach posterior level of acetabulum with blind ends directed posteriorly.

Testes deeply lobed, obliquely tandem or sometimes nearly side by side in middle of the body, preovarian; anterior testis 1.01-4.01 mm long, 1.45-4.56 mm in the dorso-ventral direction; posterior testis 1.06-4.23 mm long, 1.50-4.36 mm in the dorso-ventral direction. Seminal vesicle thin-walled and coiled; pars musculosa long, well developed, thick-walled and convoluted; pars prostatica long, well developed and almost straight (1.00-2.47 mm long, 0.50-0.62 mm wide).

Ovary subspherical, unlobed, posttesticular, dorsal to acetabulum, may be displaced on either side of the median line by the excretory vesicle when in the full state, 0.52-1.36 by 0.72-1.47 mm; Mehlis' gland close to ovary, 0.29-0.78 by 0.40-0.78 mm; Laurer's canal crosses the exretory vesicle or duct, opens on the dorsal surface about 0.5-0.9 mm posteriorly to the excretory pore; uterus forms coils running forward dorsal to the testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of pharynx to acetabulum, not confluent dorso-medially; egg 115-150 by 65-90 µm.

Genital pore at a level posterior to the oesophageal bifurcation surrounded by an oval area bounded by a ridge and free of tegumental papillae; terminal genitalium of the calicophoron type (sensu Näsmark, 1937) in median sagittal section, forms a genital pillar when everted at the tip of which the genital pore opens.

Excretory vesicle dorsal to acetabulum; excretory pore opens on the dorsal surface at level of the posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 68

Calicophoron calicophorum (Fischoeder, 1901)

Näsmark, 1937

(SEM)

a. Whole worm, ventral view (scale bar = 2 mm)

b. Acetabular region (scale bar = 1 mm)

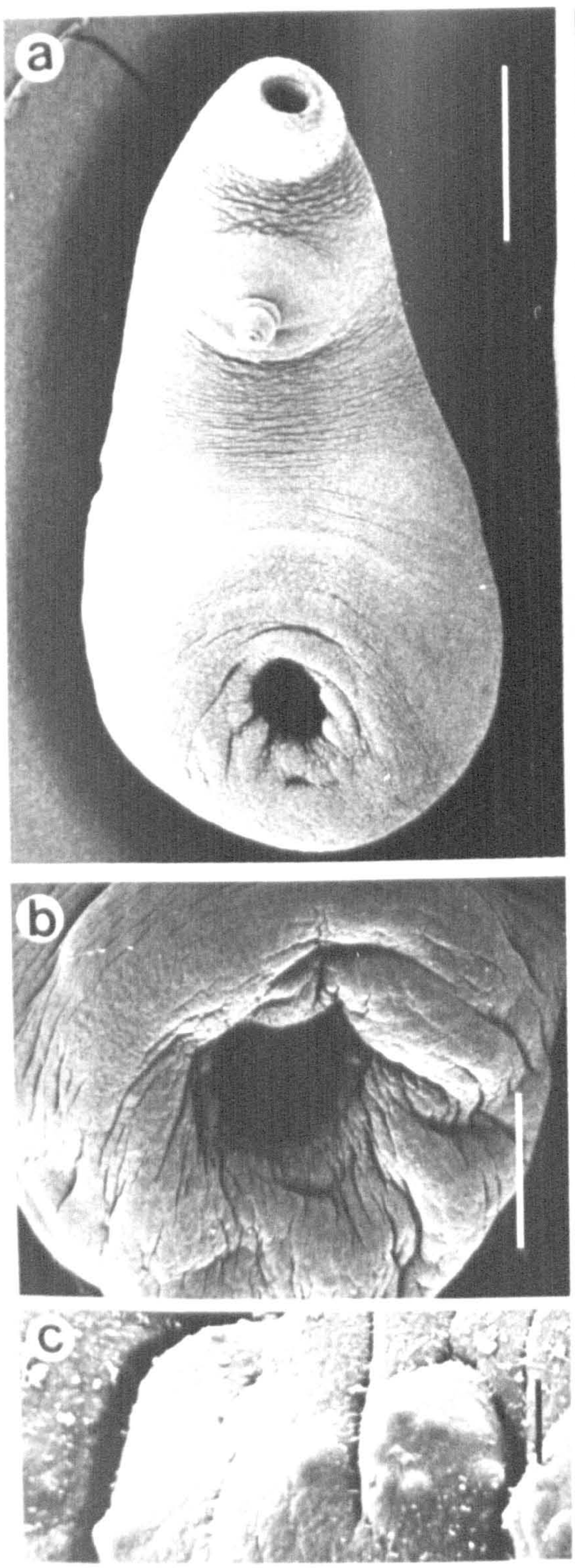
c. Small papillae found around acetabular opening
(scale bar = 20 µm)

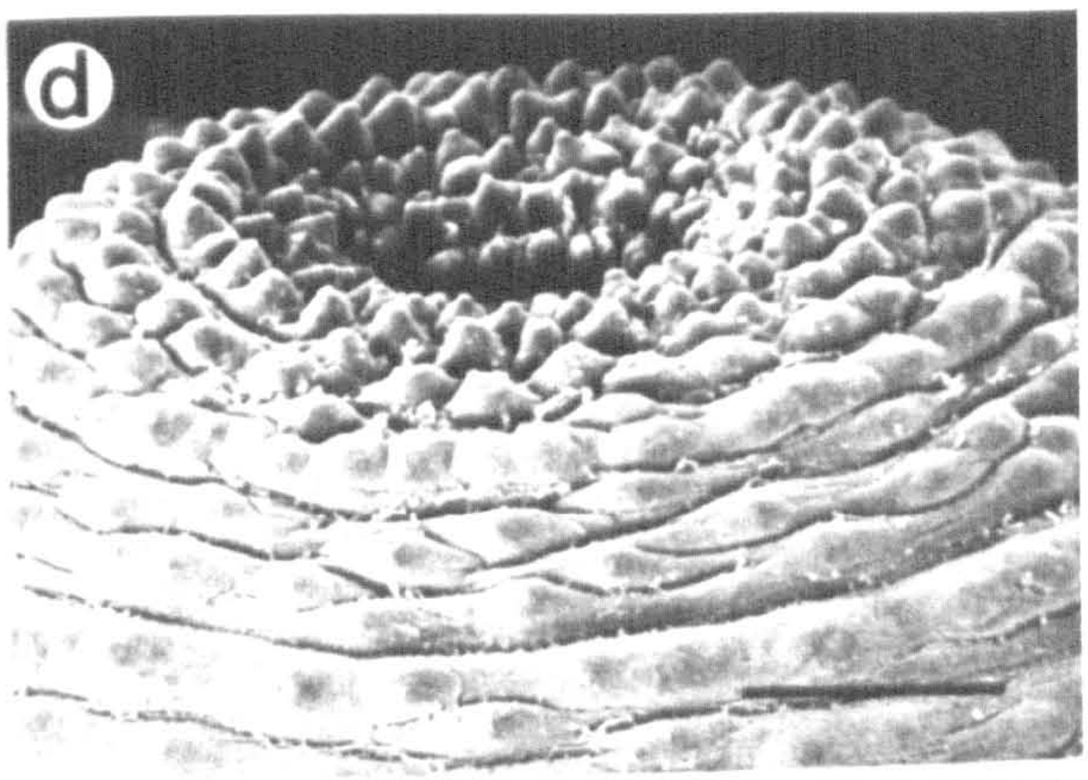
d. Anterior end showing large papillae around oral opening
(scale bar = 200 µm)

e. Closer view of papillae found around oral opening, note conical shape and smooth surface (scale bar = 39 µm)

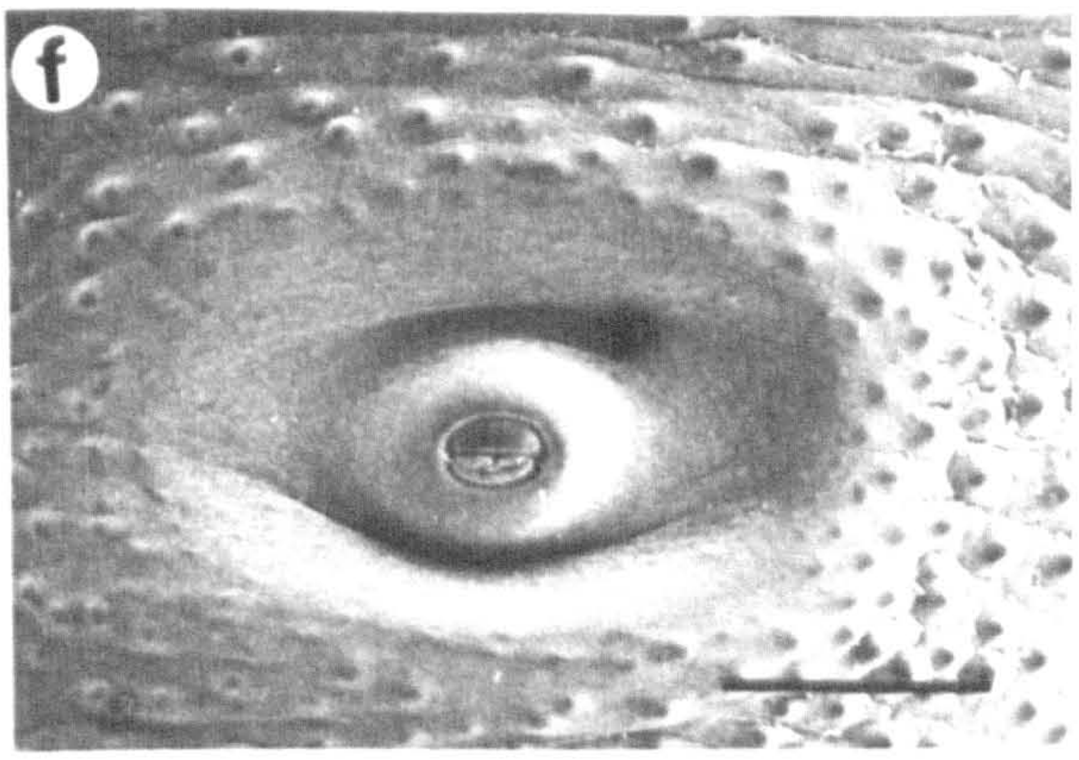
f. Genital pore region with partly everted genital pillar, note oval depression devoid of papillae
(scale bar = 300 µm)

g. Genital pore region with retracted genital pillar, note again smooth oval depression (scale bar = 300 µm)

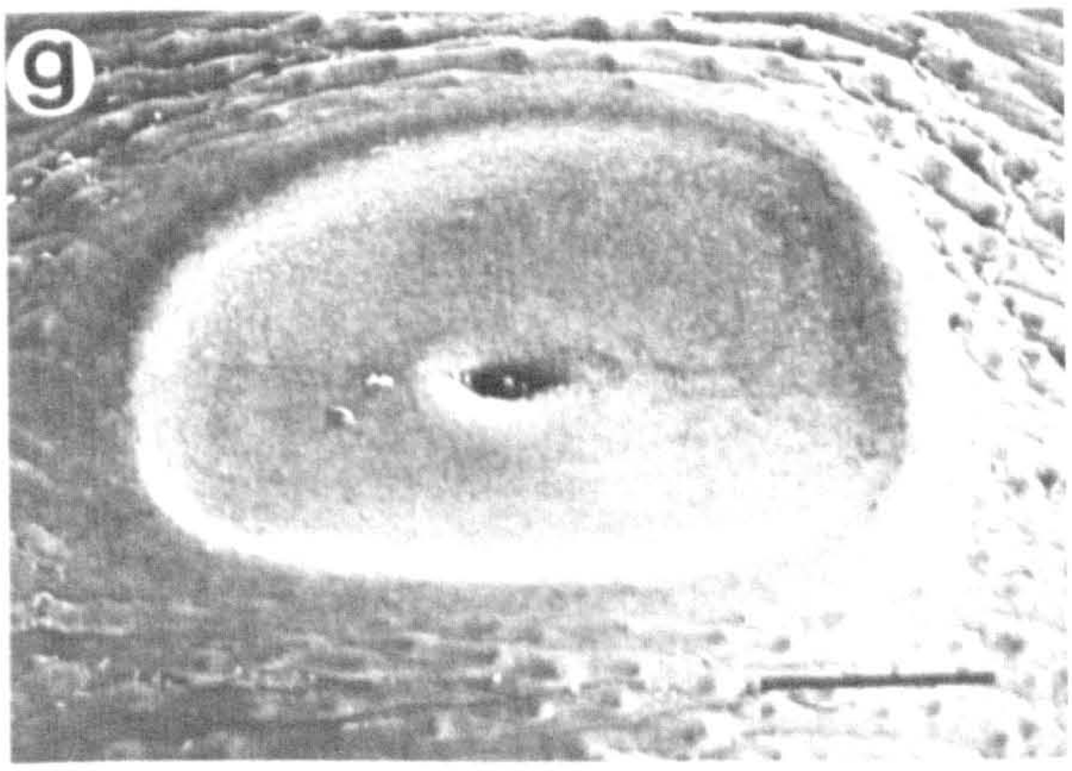

a


d


e


f

b


g

c

FIGURE 69

Calicophoron calicophorum (Fischoeder, 1901)

Näsmark, 1937

a. Whole worm, ventral view

b. Whole worm, sagittal view


a
b
3 mm

FIGURE 70

Calicophoron calicophorum (Fischoeder, 1901)

Näsmark, 1937

(median sagittal section)

a. Acetabulum (calicophoron type)

b. Pharynx (calicophoron type) and oesophagus

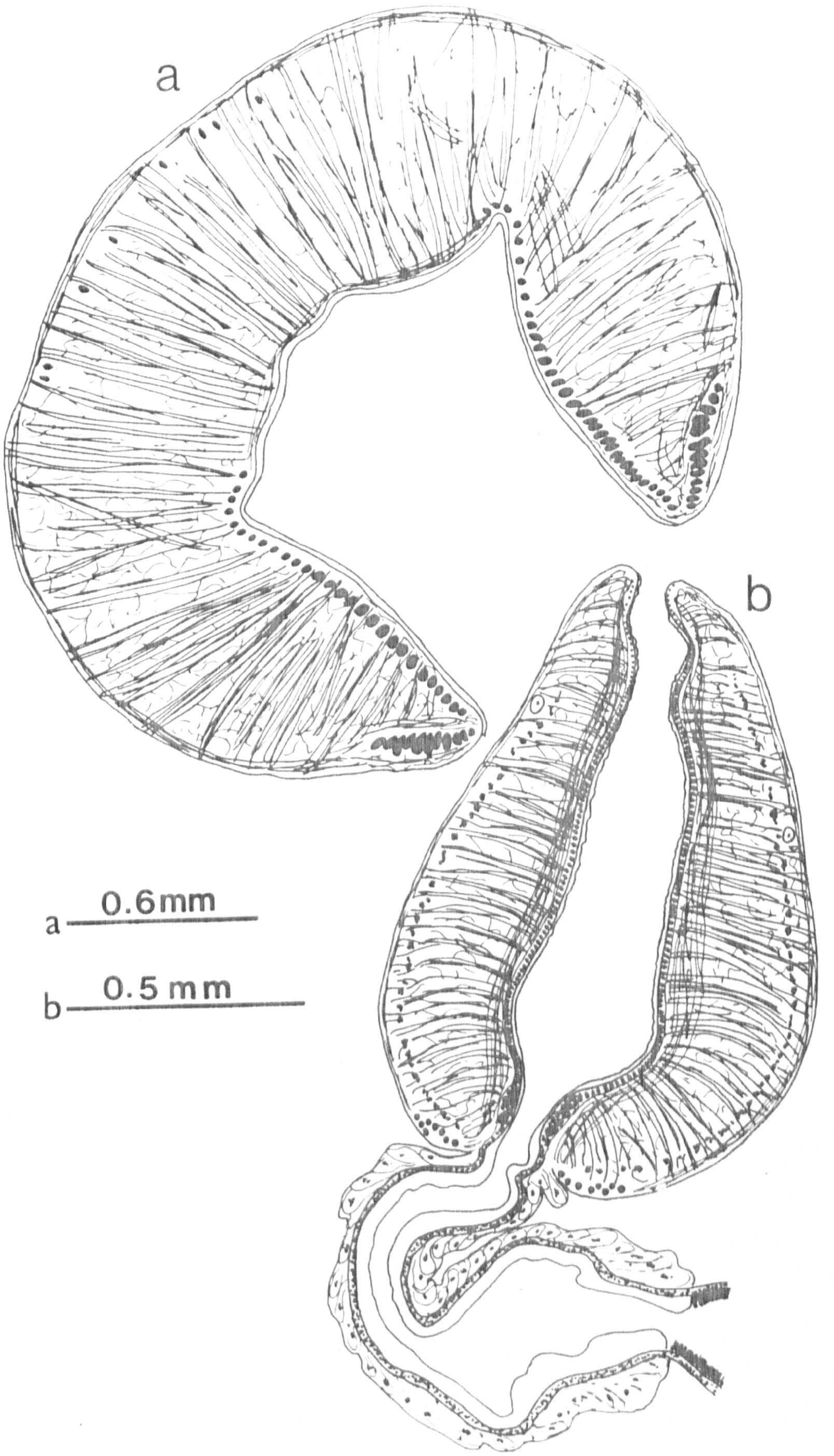

a
b
a 0.6mm
b 0.5 mm

FIGURE 71

Calicophoron calicophorum (Fischoeder, 1901)

Näsmark, 1937

(median sagittal section)

Various forms of the terminal genitalium (calicophoron type)

a. Fully everted genital pillar or column and showing also the pars prostatica

b. Retracted genital pillar

c. Fully retracted genital pillar

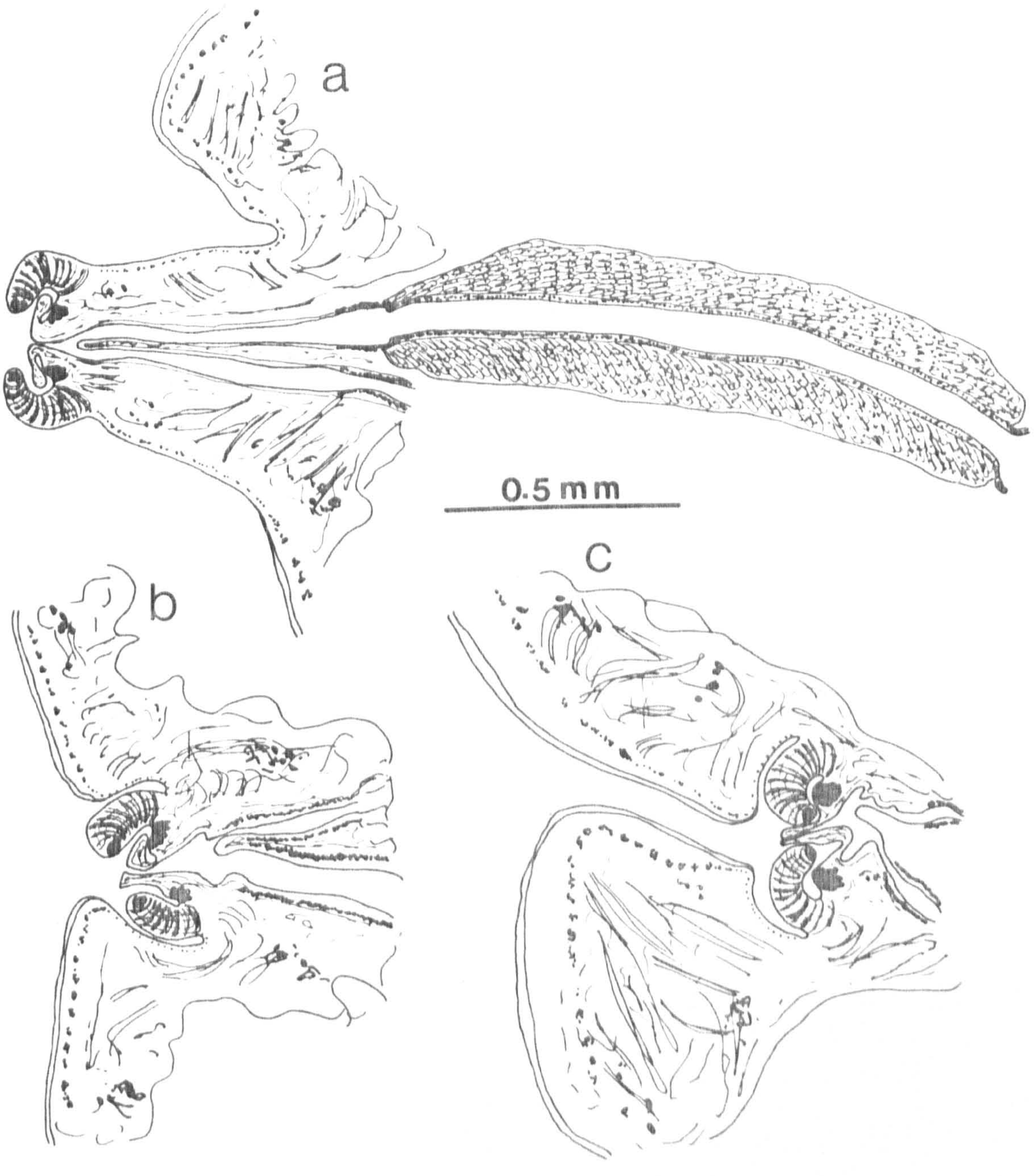

a
b
c
0.5 mm

FIGURE 72

Calicophoron calicophorum (Fischoeder, 1901)

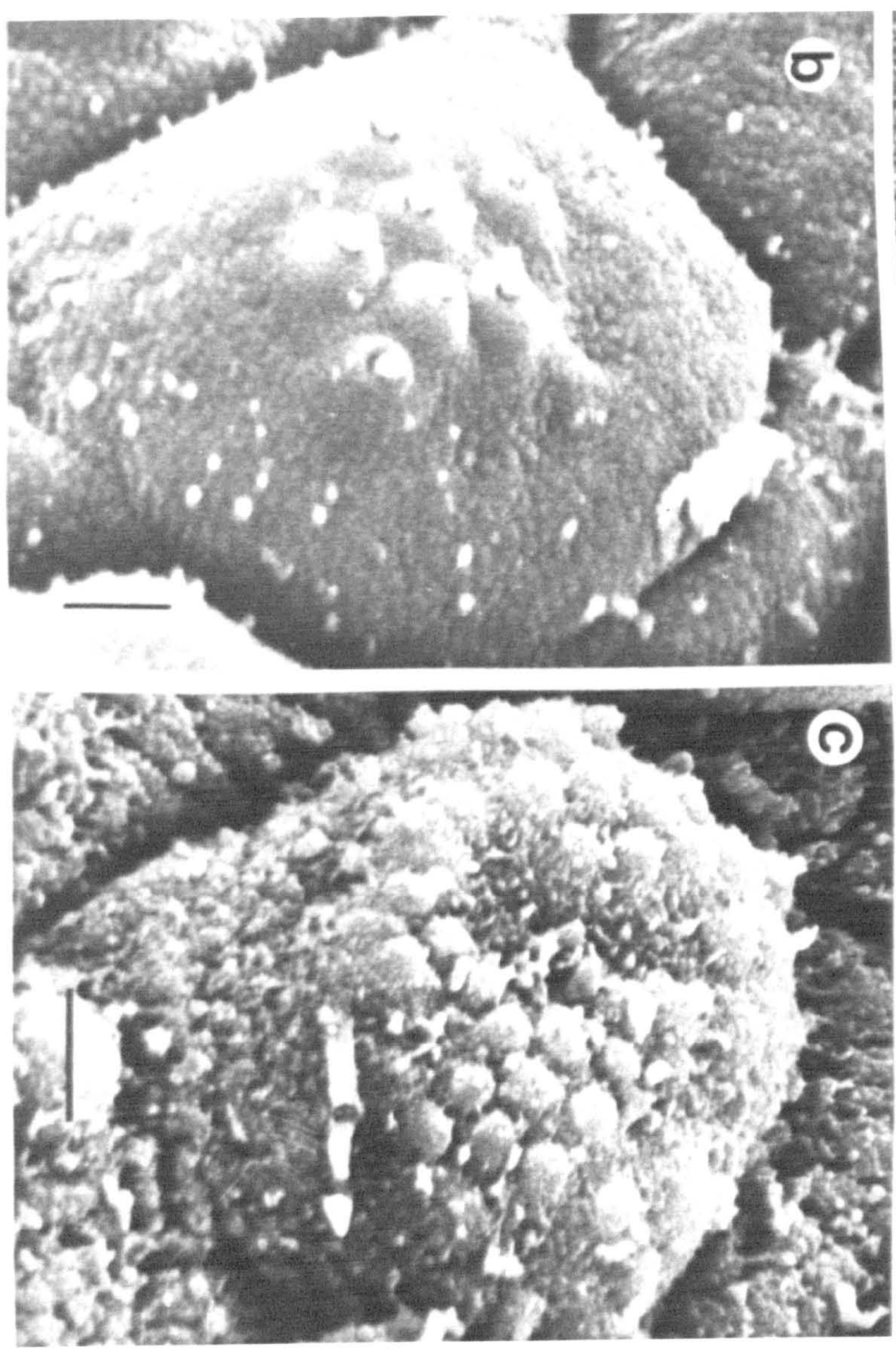
Näsmark, 1937

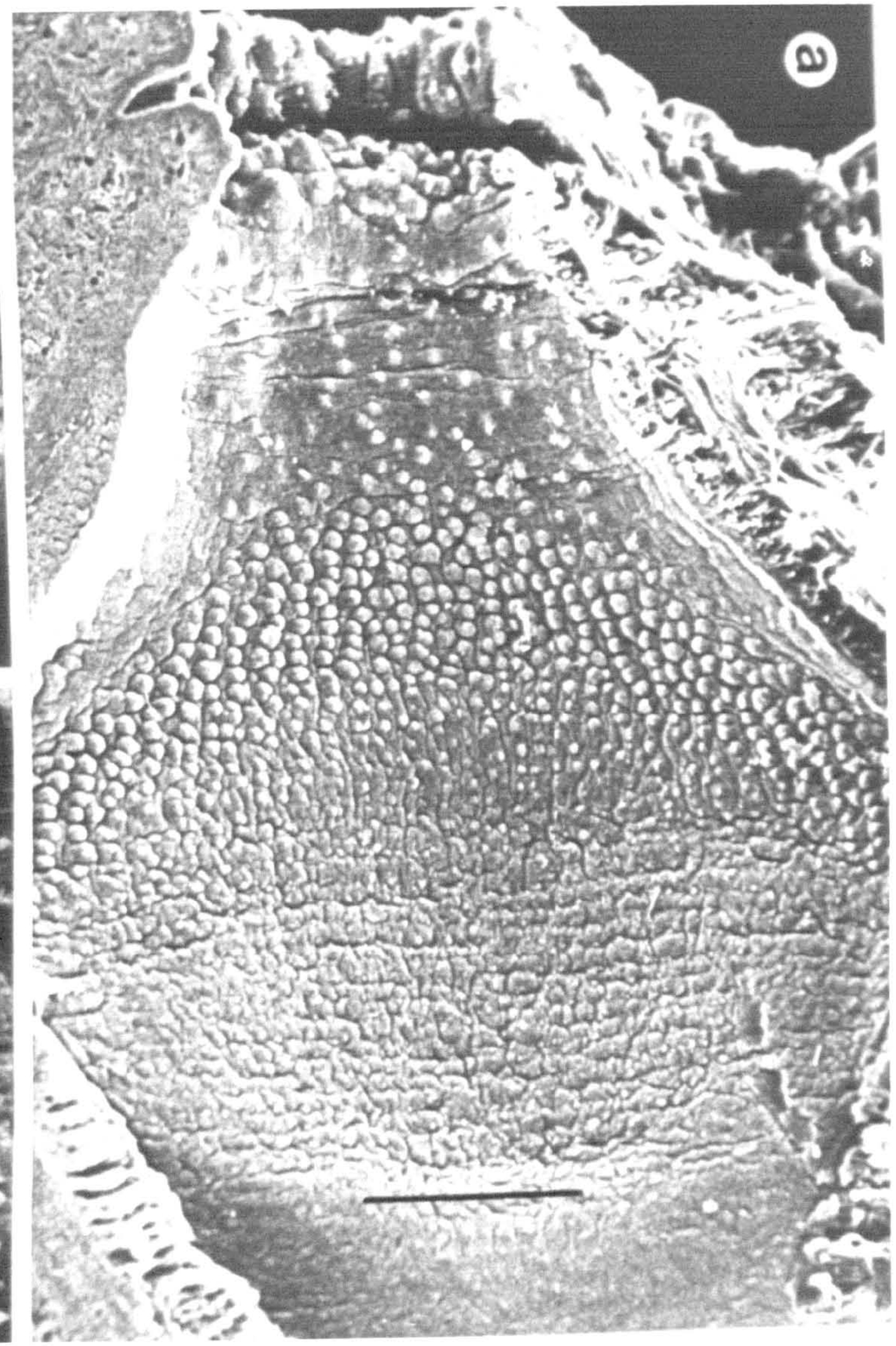
Internal surface of pharynx (SEM)

a. General view, note dome-shaped papillae on pharynx surface (scale bar = 100 µm)

b. Closer view of a papilla with few cilium-bearing structures on its apical surface (scale bar = 1 µm)

c. Closer view of another papilla with numerous cilium-bearing structures on its apical surface (scale bar = 1 µm)


b
c


a

Calicophoron bothriophoron (Braun, 1892) n. comb.

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos indicus	Mwanza, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Cattle	Tanarive abattoir, Madagascar	Commonwealth Institute of Helminthology, Dr, J.A. Dinnik collection.
	Mauritius	London School of Hygiene & Tropical Medicine coll. no. 702.
	Merca, Somalia	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Capra hircus	Nanyuki, Kenya	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Kobus defassa	Kenya	Dr. J. Grootenhuis
	Manyama, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collections.
Sheep	Nanyuki, Kenya	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.

HABITAT: Rumen and reticulum

DESCRIPTION:

Body conical, 5.12-7.36 mm long, 2.19-2.83 mm in the dorso-ventral direction. Tegumental papillae present on the anterior end of the body around the oral opening.

Acetabulum subterminal, external diameter 0.92-1.45 mm in the dorso-ventral direction; ratio to body length 1:4.2 to 1:6.3; of the pisum type in median sagittal section (sensu Näsmark, 1937); number of circular muscle units, d.e.c.1, 10-16; d.e.c.2, 6-10; v.e.c., 11-17; v.i.c., 36-44; m.e.c., 15-25.

Pharynx 0.58-0.69 mm long, 0.57-0.63 mm in the dorso-ventral direction; ratio to body length 1:9.8 to 1:10, to the diameter of the acetabulum 1:1.8 to 1:2.3; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section; internal surface lined by small dome-shaped papillae. Oesophagus 0.58-0.69 mm long, may bend dorsally, musculature of wall moderate and uniform in thickness, no bulb or posterior sphincter; lumen has two kinds of lining: about anterior one third is lined by hyaline layer and the rest is lined by ciliated epithelium similar to that found in the caeca; caeca in lateral sides of the body, form dorso-ventral bends in their course, reach level of acetabulum with the blind ends directed dorsally.

Testes deeply lobed, directly tandem in the posterior two third of the body; anterior testis 0.71-0.89 mm long, 0.65-1.38 mm in the dorso-ventral direction; posterior testis 0.75-1.32 mm long, 0.43-1.36 mm in the dorso-ventral direction; seminal vesicle deeply coiled and thin-walled; pars musculosa well developed, thick-walled and convoluted; pars prostatica well developed, 0.37-0.50 mm long, 0.17-0.30 mm wide.

Ovary subspherical, 0.32-0.60 by 0.37-0.57 mm, in between testes and acetabulum; Mehlis' gland close to ovary, 0.30-0.45 by 0.34-0.50 mm; uterus winds forward dorsal to the testes then ventral to the male ducts; Laurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface about 0.66-1.02 mm posteriorly to the excretory pore; vitellaria in lateral fields, extend from level posterior to the oesophageal bifurcation to the level of the acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 135-152 by 62-74 µm.

Genital pore at a level posterior to the oesophageal bifurcation; terminal genitalium of the bothriophoron type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level of the posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 73

Calicophoron bothriophoron (Braun, 1892) n. comb.

a. Whole worm, ventral view

b. Whole worm, sagittal view

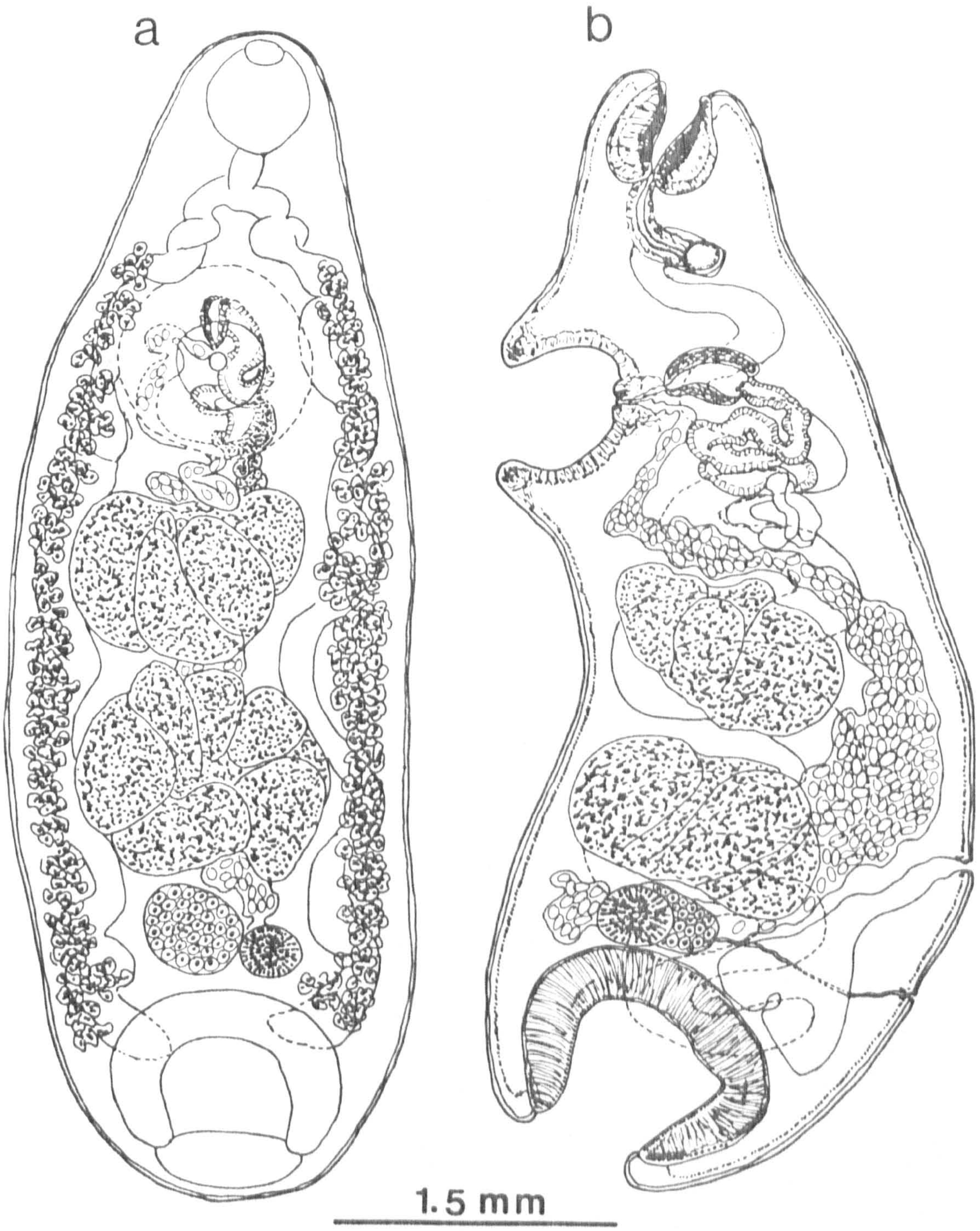

a
b
1.5 mm

FIGURE 74

Calicophoron bothriophoron (Braun, 1892) n. comb.

(median sagittal section)

a. Acetabulum (pisum type)

b. Pharynx (calicophoron type) and oesophagus. Note lumen of oesophagus with two kinds of lining, hyaline layer on anterior part and ciliated epithelium on posterior part.

c. Terminal genitalium (bothriophoron type) with normally relaxed genital papilla.

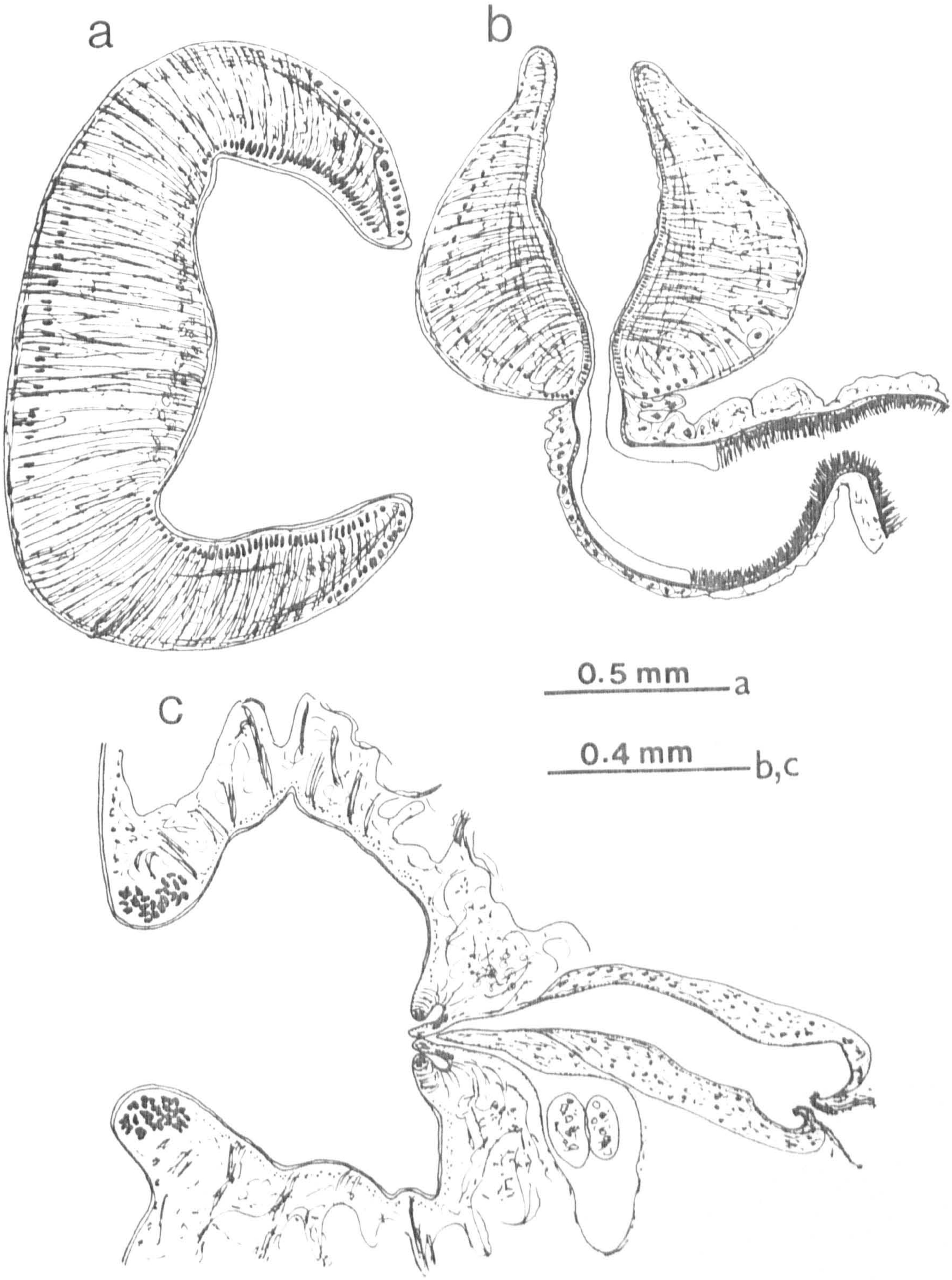

a
b
0.5 mm
a
0.4 mm
b,c
C

FIGURE 75

Calicophoron bothriophoron (Braun, 1892) n. comb.

(median sagittal section)

a - b. Terminal genitalium (bothriophoron type) with retracted genital papilla and showing also the pars prostatica.

a

0.4 mm

b

Calicophoron microbothrium (Fischoeder, 1901) n. comb.

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collections

Aepyceros melampus	Botswana	Onderstepoort Veterinary Research Institute coll. no. 7760, presented by Dr. I. Horak.
	Zimbabwe (formerly Rhodesia)	Commonwealth Institute of Helminthology coll. no. 2452.
Alcelaphus buselaphus cokei	Mazabuka, Zambia	London School of Hygiene & Tropical Medicine, Dr. P. L. LeRoux collection.
Bos indicus	Chari, Baguirmi, Chad	Dr. F. Bertin
Bos taurus	Republic of South Africa	Onderstepoort Veterinary Research Institute coll. no. S1487, presented by Dr. I. Horak.
	Sardinia	Dr. S. Teodoro, labeled "P. cervi".
Cattle	Botswana	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik's collection.
	Cairo, Egypt	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
	Iraq	Commonwealth Institute of Helminthology coll. no. 216.

Cattle	Kenya	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Mozambique	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
	Republic of South Africa	London Schoo of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Capra hircus	Angola	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Corsica	London School of Hygiene & Tropical Medicine
Damaliscus dorcas dorcas	Cape Town, Republic of South Africa	Onderstepoort Veterinary Research Institute coll. no. S2157, presented by Dr. I. Horak.
Hippotragus equinus	Cape Town, Republic of South Africa	Ondertepoort Veterinary Research Institute coll. no. S2157, presented by Dr. I. Horak.
	Transvaal, Republic of South Africa	Onderstepoort Veterinary Research Institute coll. no. S492, presented by Dr. I. Horak.
	Sudan	Dr. L.F. Khalil
Kobus leche	Zimbabwe	Commonwealth Institute of Helminthology
Ovis sp.	Iraq	Commonwealth Institute of Helminthology coll. no. 218.

Ovis sp.	Republic of South Africa	Onderstepoort Veterinary Research Institute coll. no. S153, labeled " P. cervi" presented by Dr. I. Horak.
Sheep	Angola	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Cairo, Egypt	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
	Baghdad, Iraq	London School of Hygiene & Tropical Medicine coll. no. 2169.
	Cape Town, Republic of South Africa	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
	Mazabuka, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Redunca redunca	Lake Rukwa, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Taurotragus oryx	Nairobi, Kenya	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Zimbabwe	Commonwealth Institute of Helminthology

HABITAT: Rumen and reticulum

DESCRIPTION:

Body conical, 3.80-12.50 mm long, 1.60-4.20 mm in broadest width in the dorso-ventral direction. Body surface has large dome-shaped papillae densely arranged around the oral opening and ventrally from this point to about the middle of the body. Much smaller papillae occur randomly around the acetabular opening.

Acetabulum subterminal, external diameter 1.14-2.60 mm in the dorso-ventral direction; ratio to body length 1:3.3 to 1:4.7; of the paramphistomum type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 11-18; d.e.c.2, 26-42; d.i.c., 34-56; v.e.c., 13-20; v.i.c., 40-61; m.e.c., 10-15.

Pharynx pear-shaped, broad posteriorly and tapers anteriorly, 0.47-1.38 mm long, 0.66-0.93 mm in the dorso-ventral direction; ratio to body length 1:6.1 to 1:11.4; to the diameter of the acetabulum 1:1.08 to 1:2.4; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section; internal surface lined by small dome-shaped papillae.

Oesophagus 0.47-0.85 mm long, almost straight in well relaxed specimens but bends dorsally in contracted ones, musculature of wall moderate and uniform in thickness, no bulb or posterior sphincter, lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form six dorso-ventral bends, reach level of acetabulum with blind ends directed dorsally and meet medially.

Testes deeply lobed, directly tandem in posterior half of the body; anterior testis 0.14-1.97 mm long, 0.25-2.76 mm in the dorso-ventral direction; posterior testis 0.62-2.00 mm long, 1.14-2.87 mm in the dorso-ventral direction. Seminal vesicle deeply coiled and

thin-walled; pars musculosa well developed, thick-walled and convoluted; pars prostatica barrel-shaped, almost as long as it is wide (0.13-0.67 by 0.13-0.46 mm).

Ovary subspherical, 0.56-0.79 by 0.56-0.96 mm, posttesticular, on the right or left of the median line; Mehlis' gland close to ovary, 0.28-0.52 by 0.34-0.62 mm; Laurer's canal drosses the excretory vesicle or duct and opens on the dorsal surface about 0.38-0.96 mm posteriorly to the excretory pore; uterus winds forward dorsal to testes then ventral to the male duct; vitellaria follicular in lateral fields, extend from level of pharynx or oesophagus to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 153-206 by 79-98 µm.

Genital pore at level posterior to the oesophageal bifurcation; terminal genitalium of the microbothrium type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level of the posterior border of the posterior testis and anteriorly to the opening of the Laurer's canal.

FIGURE 76

Calicophoron microbothrium (Fischoeder, 1901) n. comb.

(SEM)

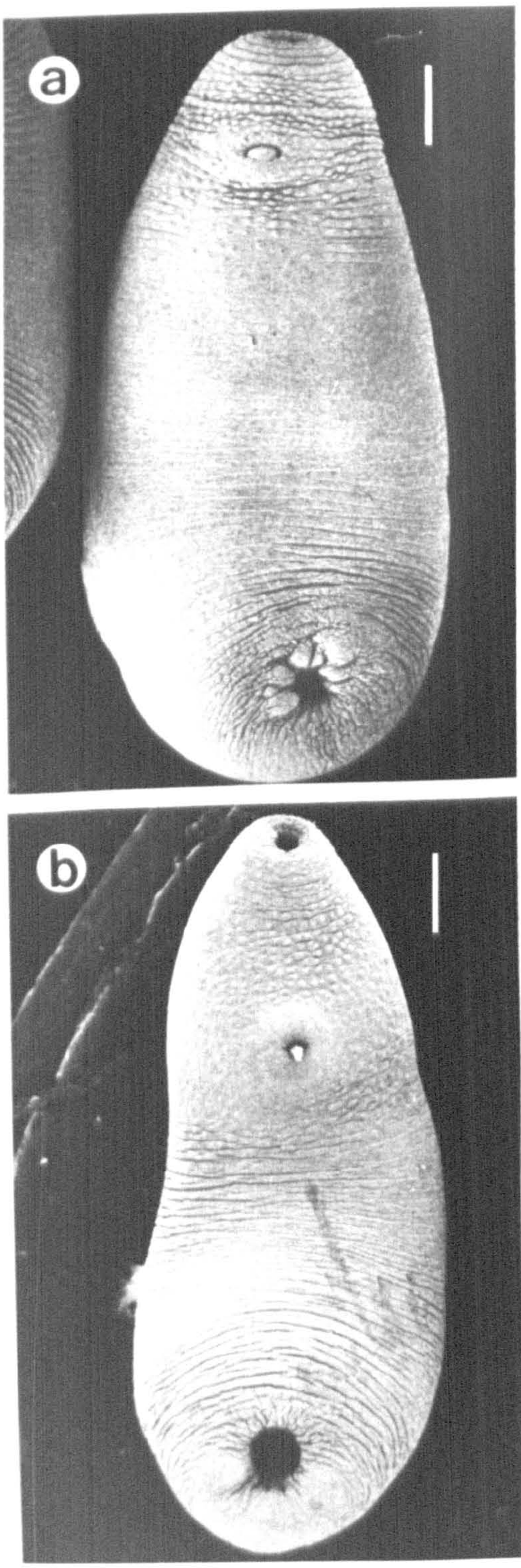
a. Whole worm, three-year old specimen recoverd from experimentally infected cattle (Dr. J.A. Dinnik's experiment), ventral view.(scale bar = 500 µm).

b. Whole worm, 124-day old specimens recovered from experimentally infected cattle (Dr. J.A. Dinnik's experiment), ventral view (scale bar = 300 µm).

c. Genital pore region with genital papilla partly everted. Note large papillae (scale bar = 100 µm)

d. Genital pore region with genital papill fully retracted (scale bar = 100 µm)

e. Small papillae found around acetabular opening (scale bar = 10 µm)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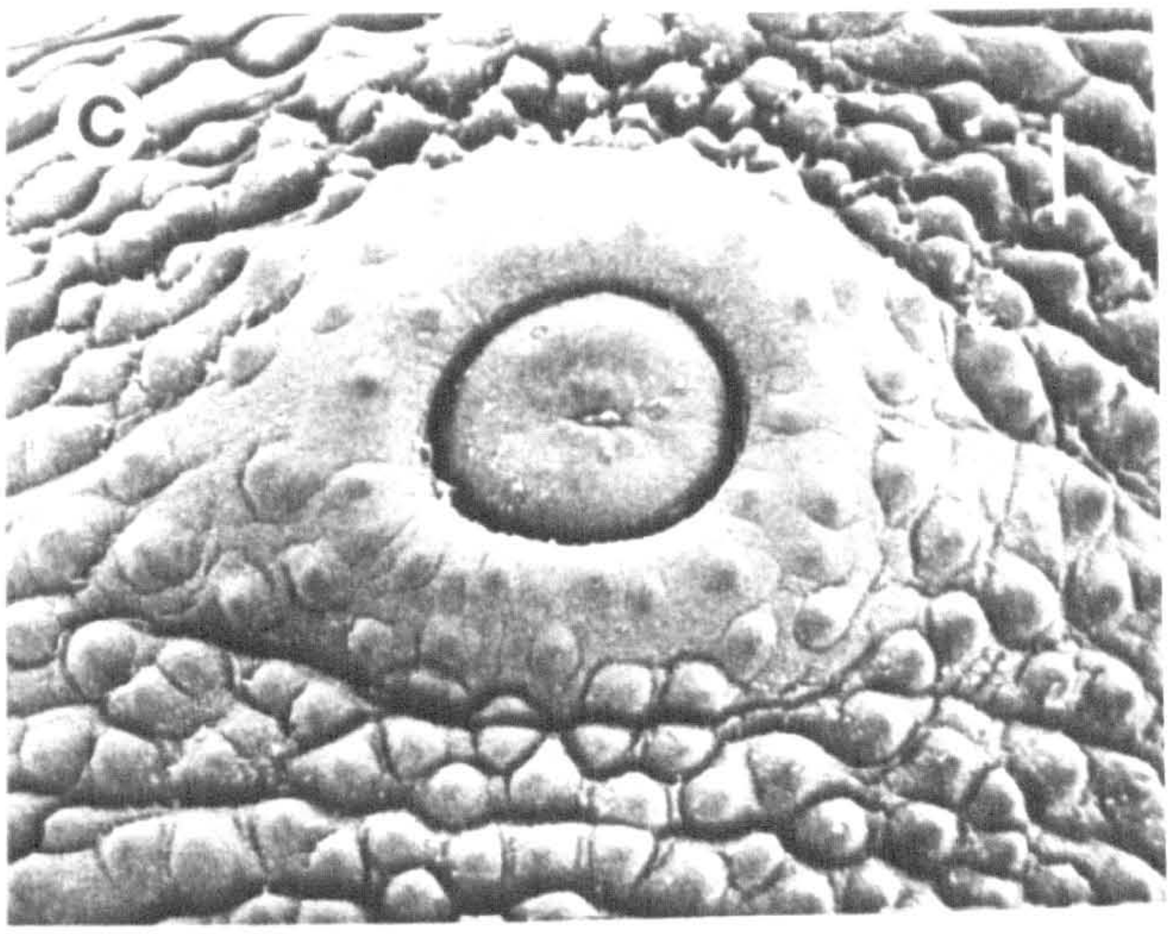
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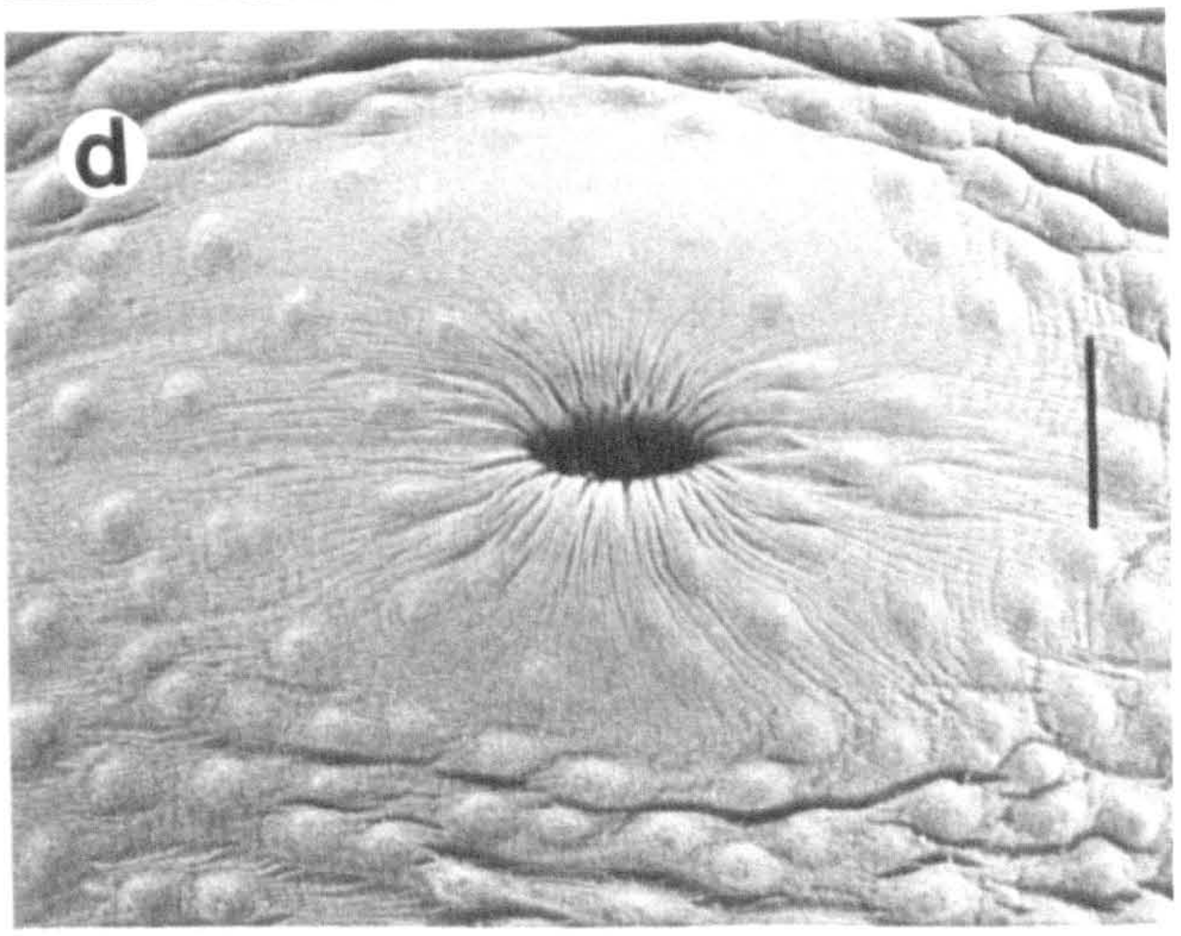
d

b

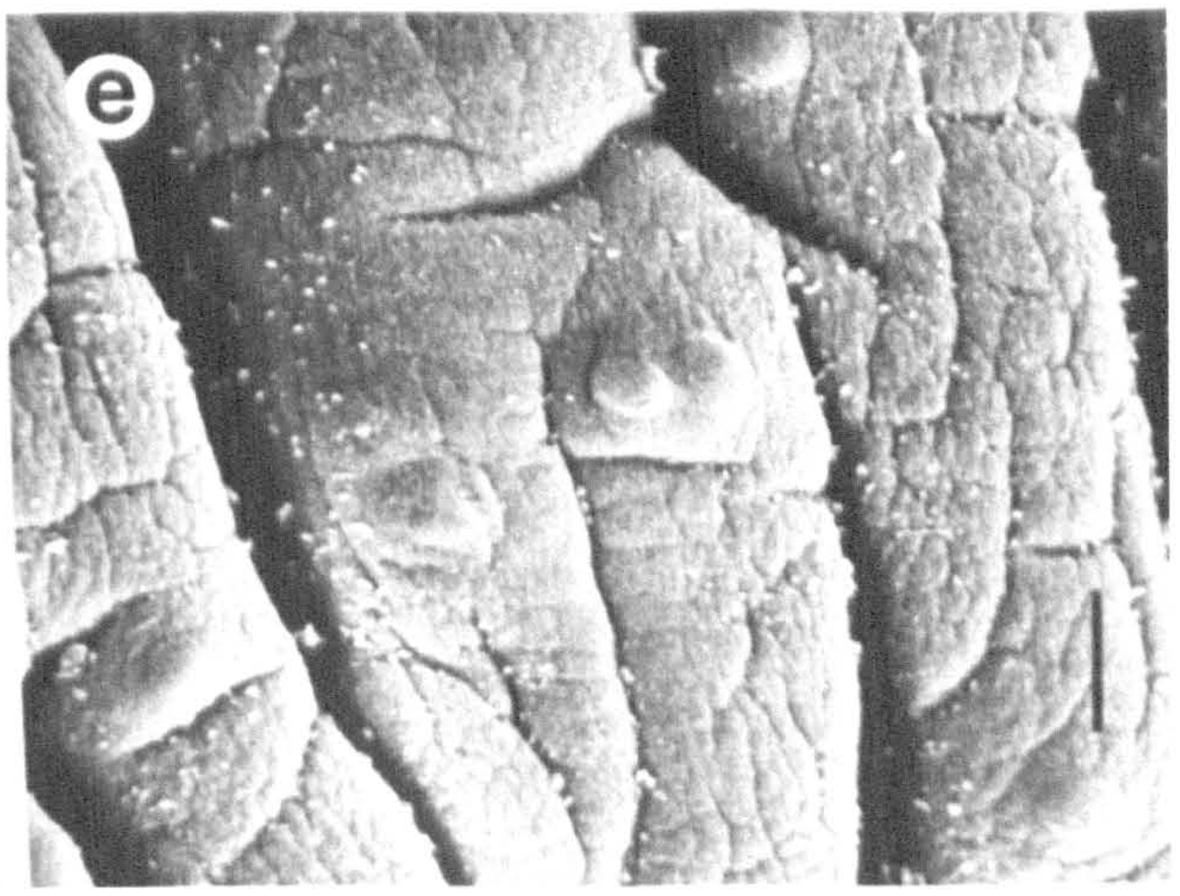
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FIGURE 77

Calicophoron microbothrium (Fischoeder, 1901) n. comb.

a. Whole worm, ventral view

b. Whole worm, sagittal view

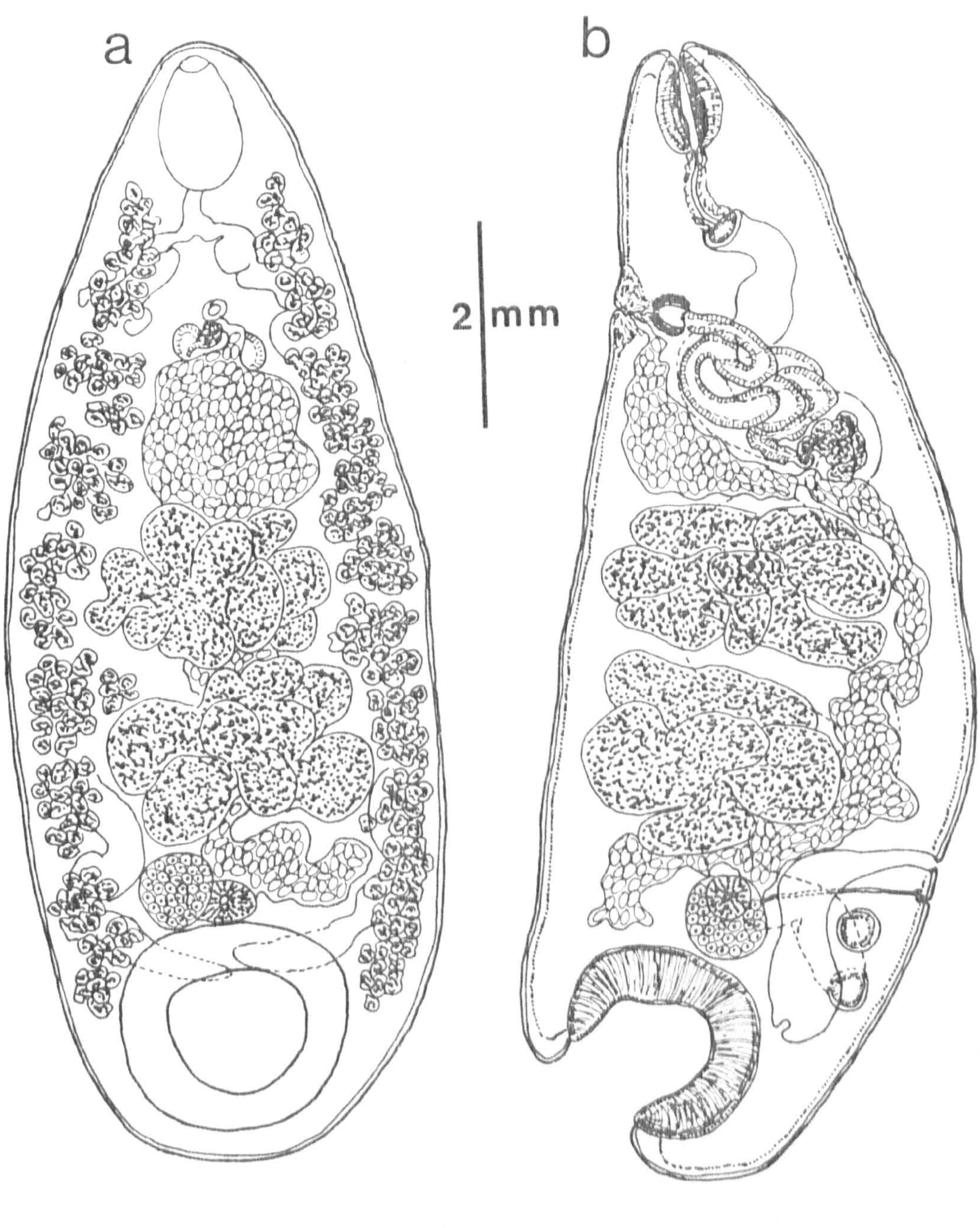

a
b
2 mm

FIGURE 78

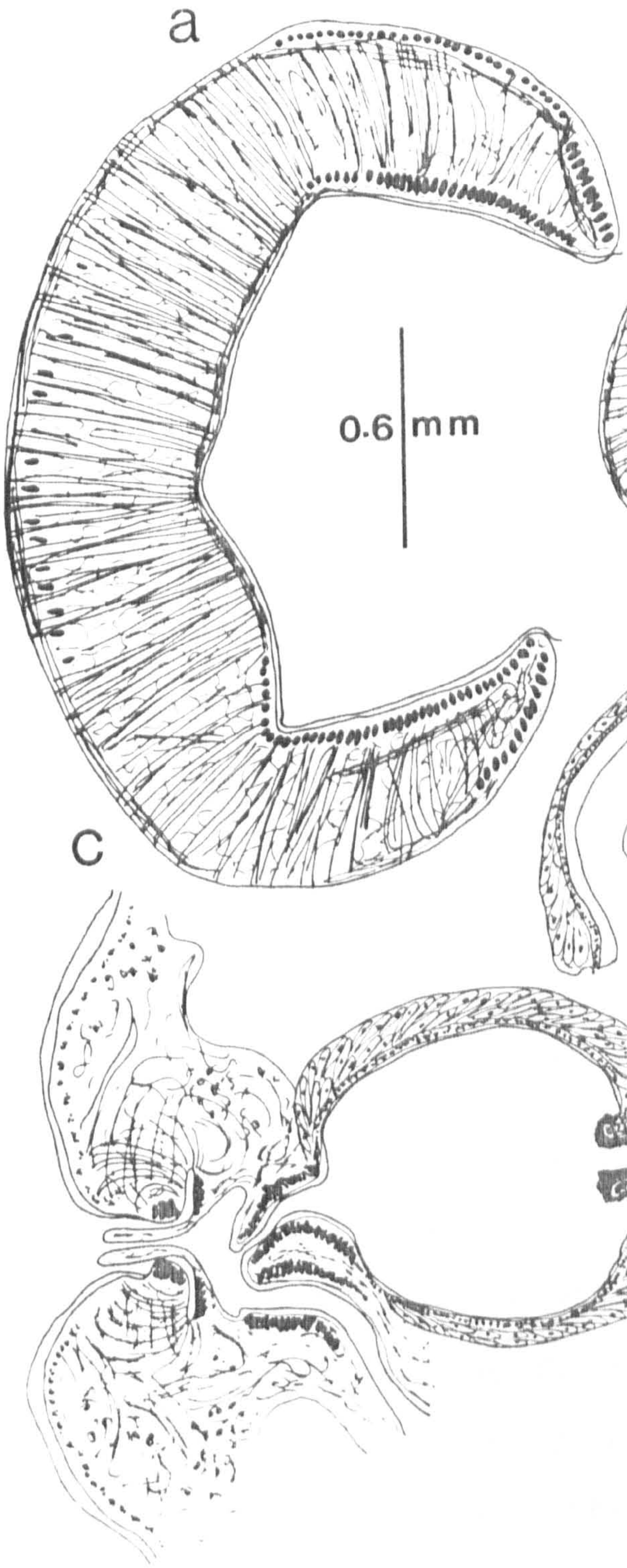
Calicophoron microbothrium (Fischoeder, 1901) n. comb.
(median sagittal section)

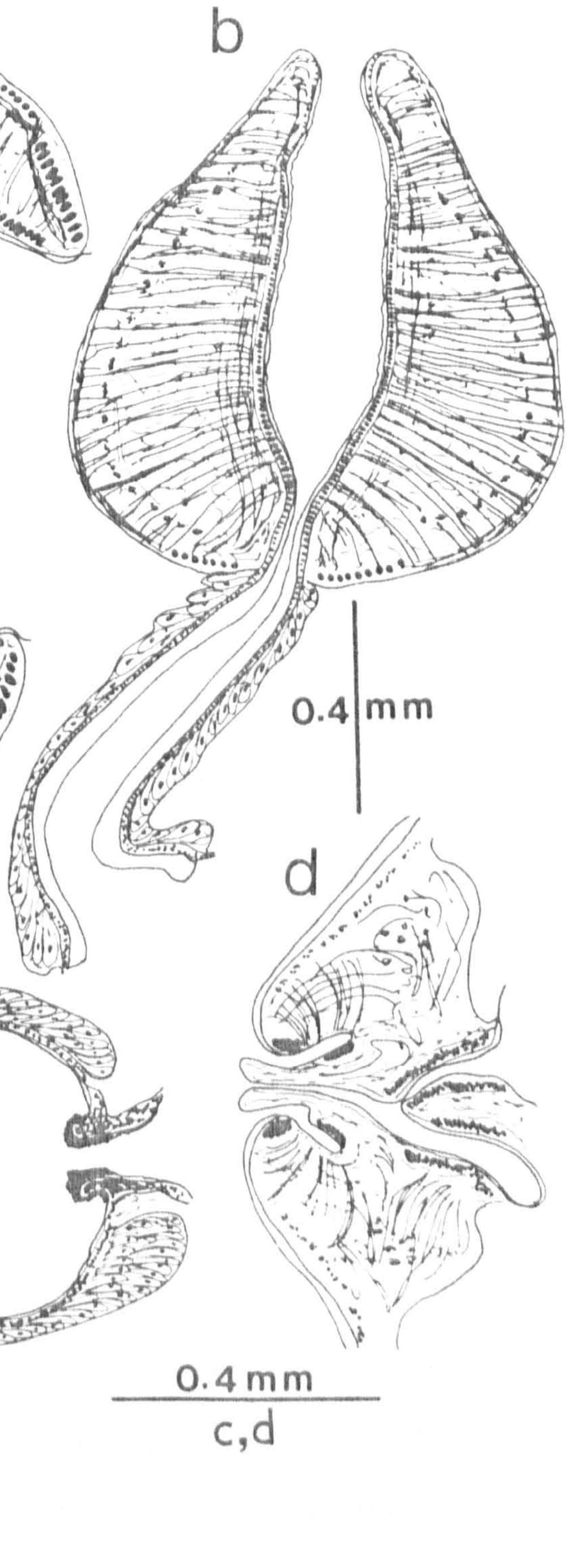
a. Acetabulum (paramphistomum type)

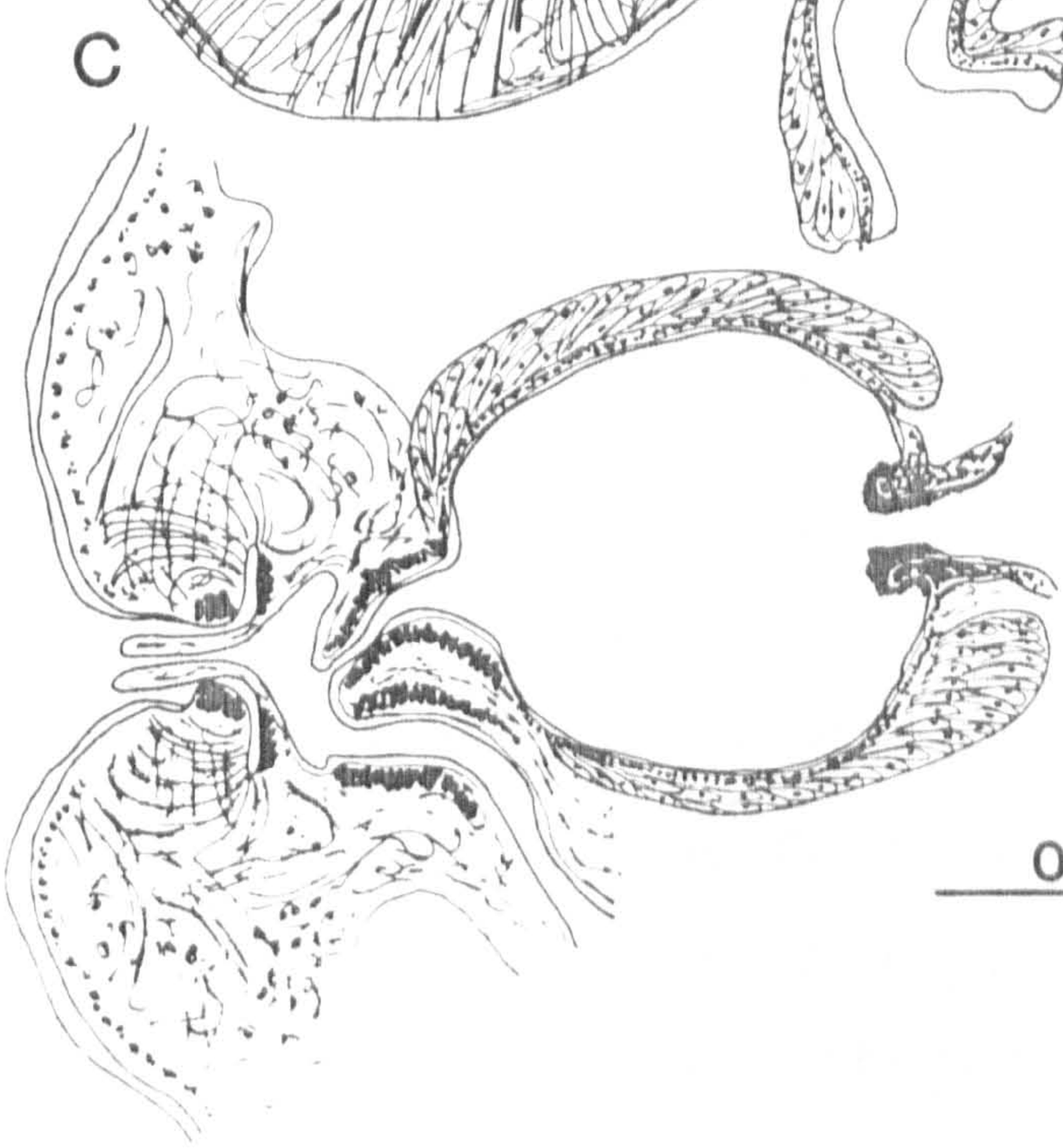
b. Pharynx (calicophoron type) and oesophagus

c. Terminal genitalium (microbothrium type) with normally relaxed genital papilla and showing also the pars prostatica.

d. Terminal genitalium (microbothrium type) with partly everted genital papilla.







0.4 mm
c,d

Calicophoron papillosum (Stiles and Goldberger, 1910) Näsmark, 1937

Synonym: Calicophoron zhejiangense Wang, 1979

TYPE SPECIMENS: United States National Parasite Collection, USDA, Beltsville, Maryland (USNMH Coll. No. 15025), from Bos indicus in Sanawaar, Punjab, India. Collected by Giles in 1883.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Bubalus bubalis	Indonesia	Mr. M.D. Brotowidjoyo
	Dacca, Bangladesh	Dr. D.I. Gibson
	India	London School of Hygiene & Tropical Medicine coll. no. 580.

HABITAT: Rumen

DESCRIPTION:

Body pear-shaped, broader at the acetabular region, 4.00-7.50 mm long, 2.10-3.35 mm in the dorso-ventral direction. Body surface has papillae present only around the oral opening and on the wall of the genital atrium.

Acetabulum subterminal, external diameter 1.42-2.01 mm in the dorso-ventral direction; ratio to body length 1:2.8 to 1:3.7; of the calicophoron type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 18-20; d.i.c., 34-39; v.e.c., 12-16; v.i.c., 40-48; m.e.c., 3-9.

Pharynx 0.80-0.87 mm long, 0.73-1.13 mm in the dorso-ventral direction; ratio to body length 1:4.6 to 1:8.6, to the diameter of the acetabulum 1:2.3 to 1:2.5; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section; internal surface has small dome-shaped papillae. Oesophagus 0.42-0.59 mm long, musculature of wall moderate and uniform in thickness, no bulb or

posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form dorso-ventral bends, reach level of acetabulum with blind ends directed postero-ventrally.

Testes deeply lobed, directly tandem in middle third of the body; anterior testis 0.31-1.01 mm long, 0.57-1.74 mm in the dorso-ventral direction; posterior testis 0.35-1.01 mm long, 0.61-2.32 mm in the dorso-ventral direction. Seminal vesicle thin-walled and coiled; pars musculosa well developed, thick-walled and convoluted; pars prostatica well developed, longer than it is wide (0.64-0.68 by 0.14-0.18 mm).

Ovary subspherical, posttesticular, at right or left of the median line, 0.17-0.29 by 0.25-0.44 mm; Mehlis' gland close to ovary at the same level of one of its lateral sides or slightly posterior to it, 0.15-0.20 by 0.17-0.19 mm; Laurer's canal crosses excretory vesicle or duct and opens on the dorsal surface about 0.47-0.59 mm posteriorly to the excretory pore; uterus winds forward dorsal to testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of oesophagus to middle of the acetabulum; egg 129-132 by 59-63 µm.

Genital pore at level posterior to the oesophageal bifurcation; terminal genitalium of the papillogenitalis type (sensu Eduardo, 1980a) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level of the posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 79

Calicophoron papillosum (Stiles and Goldberger, 1910)
Näsmark, 1937

Whole worm, sagittal view


1 mm

FIGURE 80

Calicophoron papillosum (Stiles and Goldberger, 1910; Näsmark, 1937

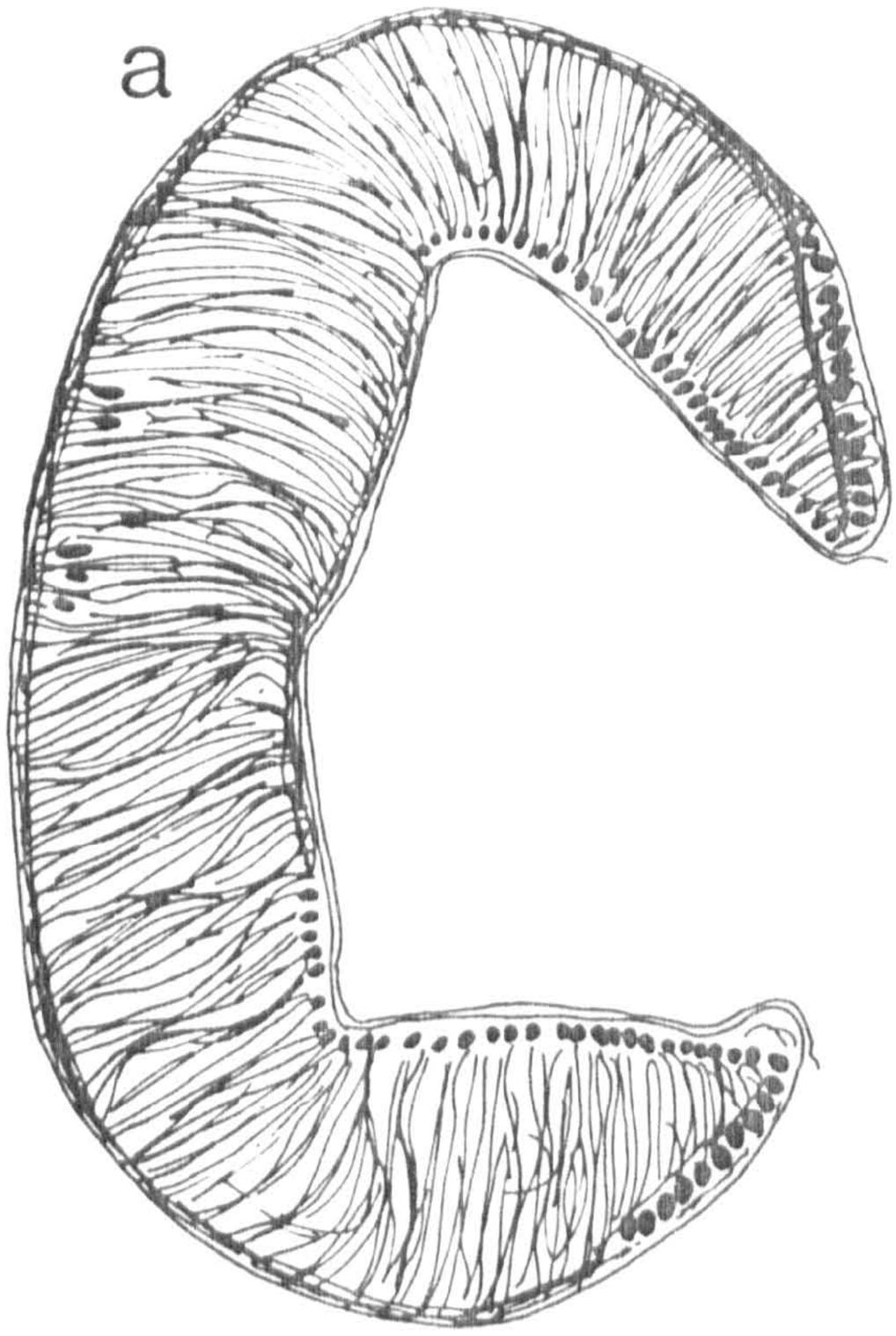
(median sagittal section)

a. Acetabulum (calicophoron type)

b. Pharynx (calicophoron type) and oesophagus

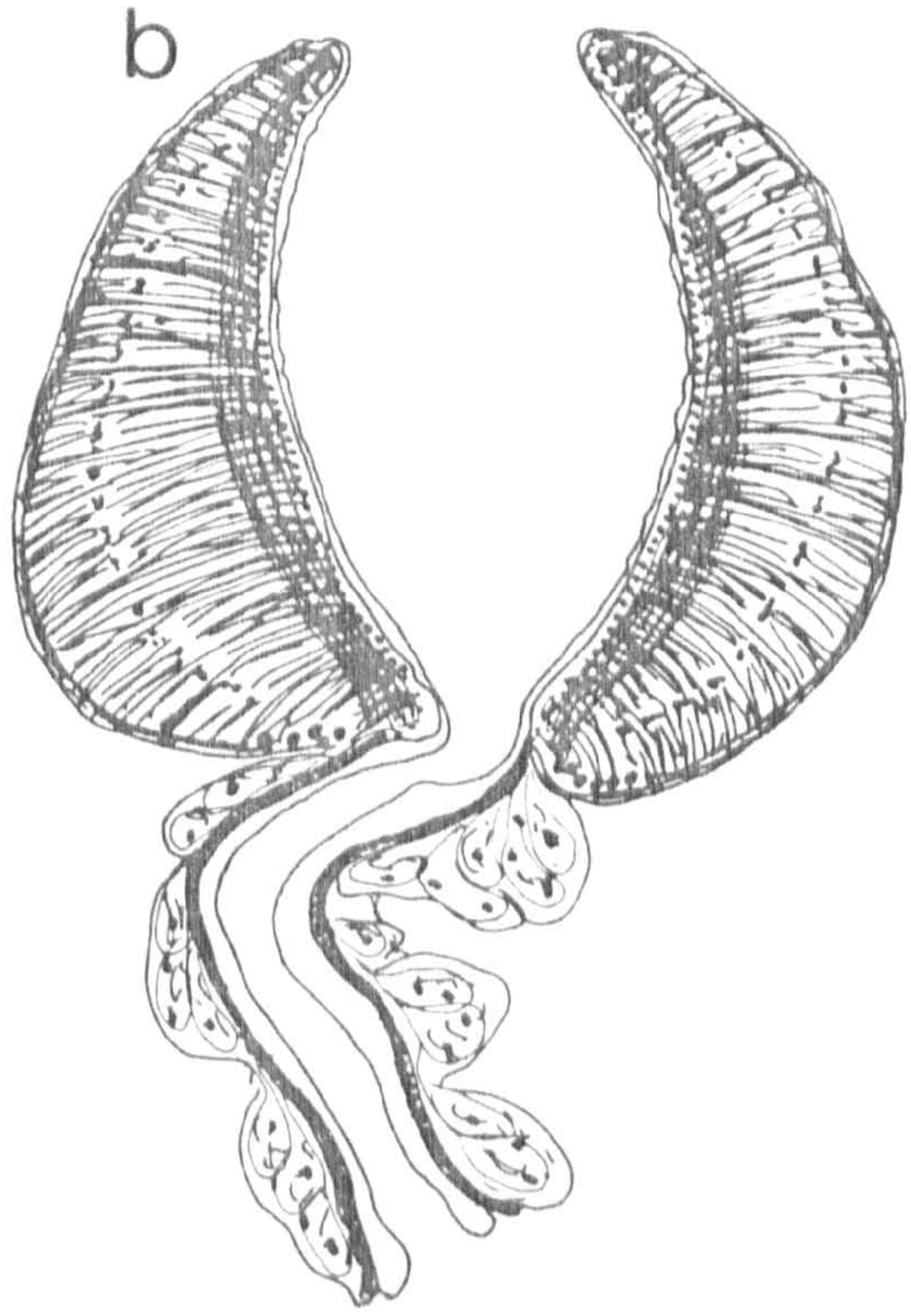
d. Terminal genitalium (papillogenitalis type)

a



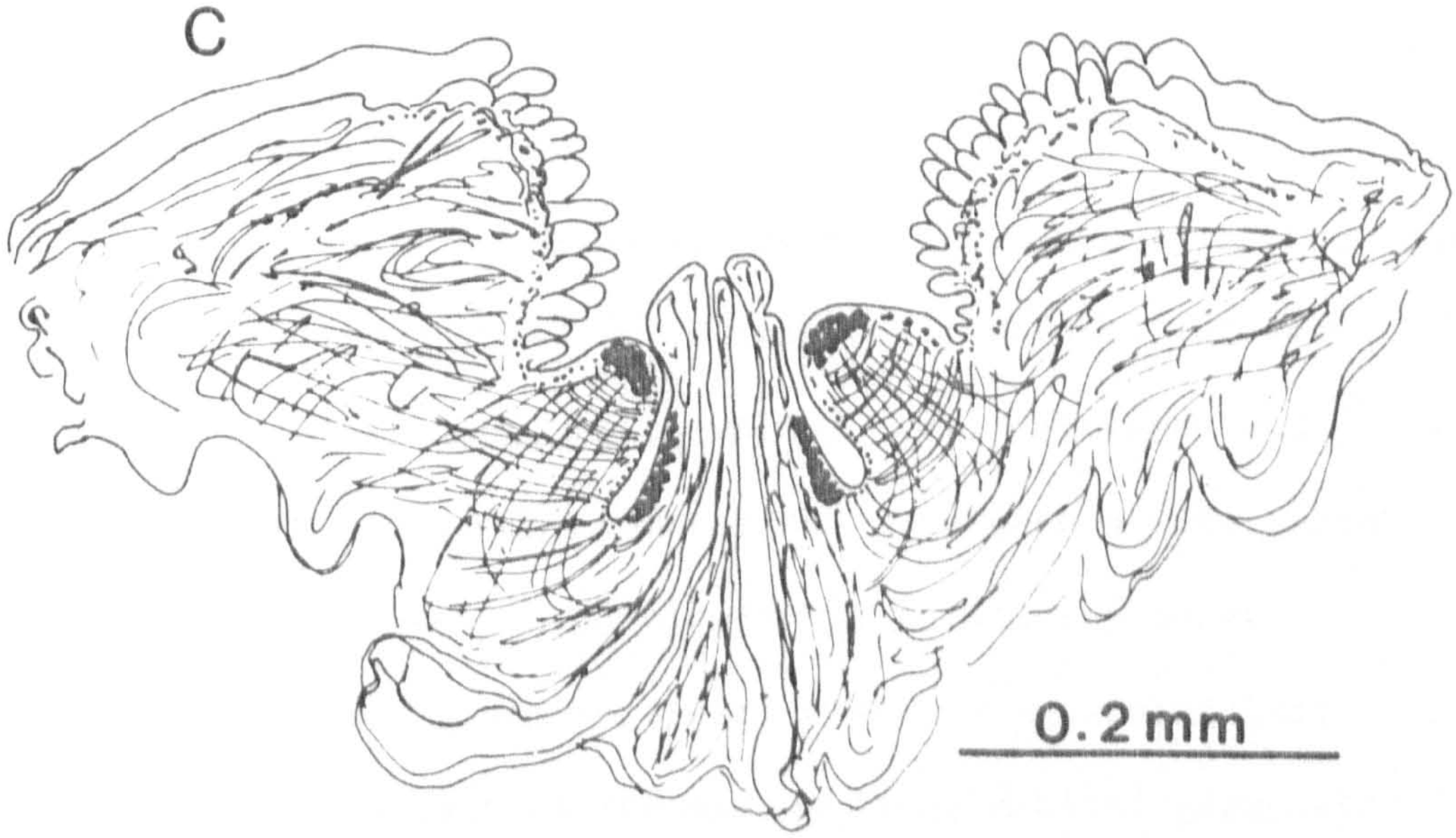
0.4mm

b



0.3mm

C



0.2mm

Calicophoron papilligerum (Stiles and Goldberger, 1910) n. comb.

TYPE SPECIMENS: Could not be traced and no other material is available for examination.

HOST: Cervus eldi

LOCALITY: Not known

HABITAT: Stomach

DESCRIPTION: From Stiles and Goldberger (1910)

Body 8.50 mm long, 4.30 mm broad near caudal end; tapers gradually to bluntly pointed oral end, very rapidly to very bluntly rounded caudal end. Surface papillae absent.

Acetabulum terminal, 1.88 mm in transverse diameter, ratio to body length 1:4.5; type in median sagittal section and number of circular muscle units could not be elucidated from the present specimen.

Pharynx oval in frontal section; type also could not be elucidated from the authors' description; internal surface papillate. Oesophagus bent dorsally, rather uniform in thickness, no bulb or posterior sphincter. Caeca wavy dorso-ventrally, extend posteriorly to about middle of acetabulum.

Testes large, lobed, tandem in posterior two third of the body; seminal vesicle dilated (0.27 mm in diameter), thin-walled and coiled; pars musculosa long, thick-walled, well developed and convoluted (about 190 µm in diameter and thickness of wall about 60 µm); pars prostatica well developed but relatively short.

Ovary and Mehlis' gland posttesticular and preacetabular; ovary slightly to the left of the median line; Mehlis' gland about median in position; uterine coils dorsal to testes then ventral to the male ducts; vitellaria consist of well developed but sparsely

scattered follicles in lateral fields of the body, extend from level of oesophagus to the level posterior to the caecal ends; Laurer's canal drosses excretory vesicle and opens on the dorsal surface posteriorly to the excretory pore; egg 135 by 67 µm.

Genital pore at a level posterior to the oesophageal bifurcation; type in median sagittal section could not be made out from the authors' description but a large ventral atrium is present whose wall is lined by papillae.

Excretory vesicle large and dorsal to acetabulum; excretory pore opens on the dorsal surface anteriorly to the Laurer's canal opening.

Calicophoron raja Näsmark, 1937

TYPE SPECIMENS: Naturhistoriska riksmuseet, Stockholm, Sweden.
From the stomach of cattle in the Sudan.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Aepyceros melampus	Botswana	Commonwealth Institute of Helminthology, coll. no. 85/79.
	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Alcelaphus buselaphus cokei	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Bos indicus	Republic of South Africa	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Bos taurus	Cuba	Dr. J. Prokopič
	Kenya	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Pretoria, Republic of South Africa	Onderstepoort Veterinary Research Institute coll. no. S1150, labeled "P. calicophorum". Presented by Dr. I. Horak.
Cattle	Botswana	British Museum (Natural History) coll. no. 1956.11. 6.5-25, labeled "P. calicophorum".

Cattle	Kenya	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
		Dr. L.F. Khalil
	Komatipoort, Republic of South Africa	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
	Mazabuka, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Capra hircus	Lochinvar, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
	Zimbabwe	London School of Hygiene & Tropical Medicine coll. no. 106, labeled "*P. cervi*".
Connochaetes taurinus	Namibia	Onderstepoort veterinary Research Institute coll. no. S169, presented by Dr. I. Horak.
	Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Mazabuka, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
	Zimbabwe	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Damaliscus korrigum	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.

Gazella thomsonii	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Kobus defassa	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Kobus leche	Botswana	British Museum (Natural History), labeled "P. cali-cophorum".
Kobus varondi	Botswana	Dr. D.I. Gibson
	Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Oryx gazelle	Namibia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Ovis sp.	Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Naval's Point, Republic of South Africa	Onderstepoort Veterinary Research Institute coll. no. 131, presented by Dr. I. Horak.
	Mbesuma, Chinsali, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Redunca redunca	Tanzania	Commonwealth Institute of Helminthology, Dr. J. A. Dinnik collection.
Syncerus caffer	Namibia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.

Syncerus caffer	Namwala, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
	Zimbabwe	London School of Hygiene & Tropical Medicine coll. no. 1187.
Taurotragus oryx	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Tragelaphus scriptus	Zimbabwe	London School of Hygiene & Tropical Medicine, Dr. P.L LeRoux collection.
Tragelaphus strepsiceros	Zimbabwe	London School of Hygiene & Tropical Medicine coll. no. 5273.

HABITAT: Rumen, reticulum and rarely abomasum

DESCRIPTION:

Body conical, bend slightly ventrally, decidedly much broader at acetabular region, 4.72-12.10 mm long, 3.39-5.05 mm in the dorso-ventral direction. Body surface has papillae around the oral opening and much smaller ones densely arranged immediately on the area around the genital pore region including the genital pillar.

Acetabulum subterminal, external diameter 1.11-3.36 mm in the dorso-ventral direction; ratio to body length 1:2.3 to 1:3.1; of the pisum type (sensu Näsmark, 1937) in median sagittal section with the d.e.c.2 units fewer in number and irregularly spaced than the d.e.c.1 units.; number of circular muscle units, d.e.c.1, 20-29; d.e.c.2, 5-15; d.i.c., 44-56; v.e.c., 21-27; v.i.c., 63-73; m.e.c., 8-13.

Pharynx 0.47-1.05 mm long, 0.69-0.90 mm in the dorso-ventral direction; ratio to body length 1:7.5 to 1:10.3, to the diameter of the acetabulum 1:2.5 to 1:2.8; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section; internal surface has small dome-shaped papillae. Oesophagus 0.73-0.70 mm long, may bend dorsally, musculature of wall moderate and uniform in thickness, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form dorso-ventral bends, reach level of acetabulum with blind ends directed dorsally.

Testes lobed, obliquely tandem in posterior half of the body; anterior testis 1.29-1.74 mm long, 2.03-3.02 mm in the dorso-ventral direction; posterior testis 1.37-2.03 mm long, 2.03-3.78 mm in the dorso-ventral direction; seminal vesicle thin-walled and coiled; pars musculosa well developed, long, thick-walled and convoluted; pars prostatica well developed, 0.70-0.96 mm long and 0.34-0.38 mm wide.

Ovary subspherical, unlobed, posttesticular, dorsal to acetabulum, 0.45-0.87 by 0.58-0.72 mm.; Mehlis' gland close to ovary, 0.37-0.38 by 0.29-0.47 mm; Laurer's canal crosses excretory vesicle or duct and opens on the dorsal surface about 1.01-1.42 mm posteriorly to the excretory pore; uterus winds forward, dorsal to testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of pharynx to acetabulum, not confluent dorso-medially in their anterior and posterior limits; egg 138-162 by 71-81 µm.

Genital pore at level posterior to the oesophageal bifurcation; terminal genitalium of the raja type (new type) characterized by

the presence of a genital pillar or column which is covered by densely arranged small tegumental papillae.

Excretory vesicle dorsal to acetabulum; excretory pore opens on the dorsal surface at level of the posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 81

Calicophoron raja Näsmark, 1937

(SEM)

a. Whole worm, ventral view (scale bar = 2 mm)

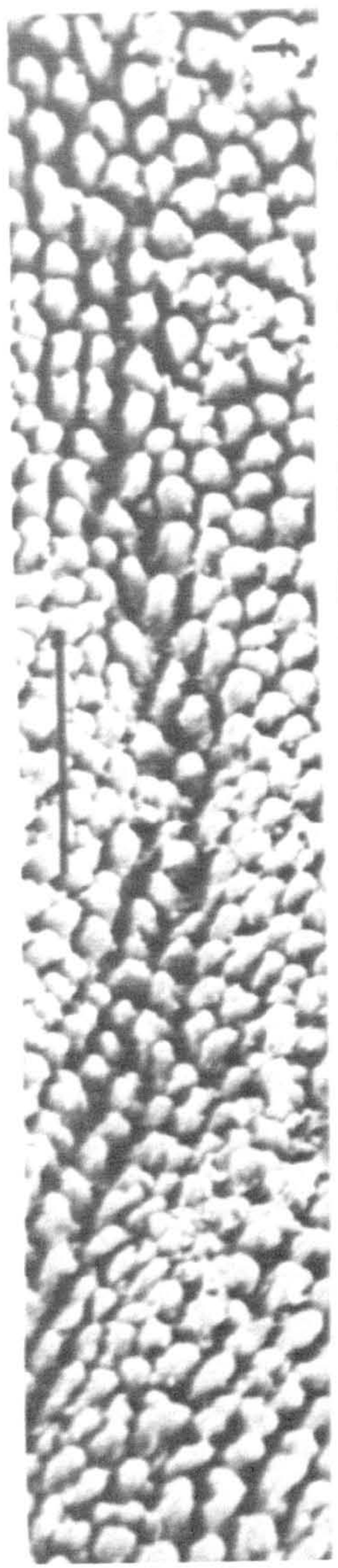
b. Anterior end, note papillae around oral opening (scale bar 200 µm)

c. Genital pore region with fully everted genital pillar or column, note very small papillae densely arranged on the surface of the pillar (scale bar = 200 µm)

d. Genital pore region with partly everted genital pillar (scale bar = 200 µm)

e. Genital pore region with fully retracted genital pillar (scale bar = 200 µm)

f. Closer view of papillae on the surface of the genital pillar (scale bar = 30 µm)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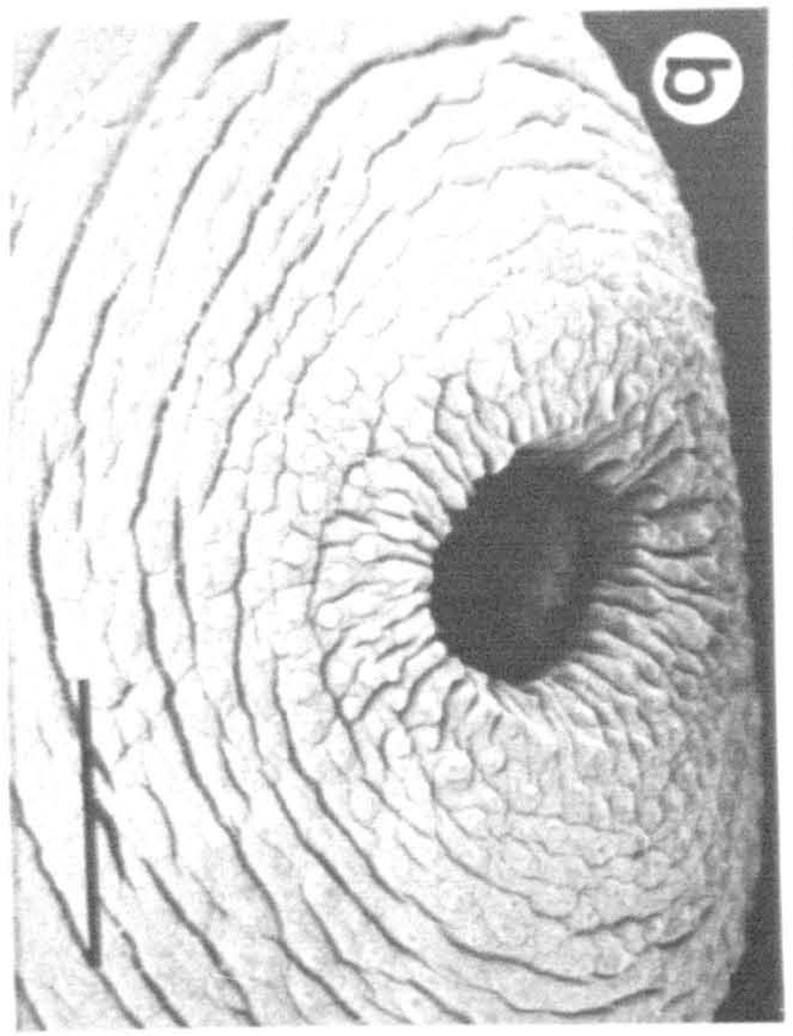
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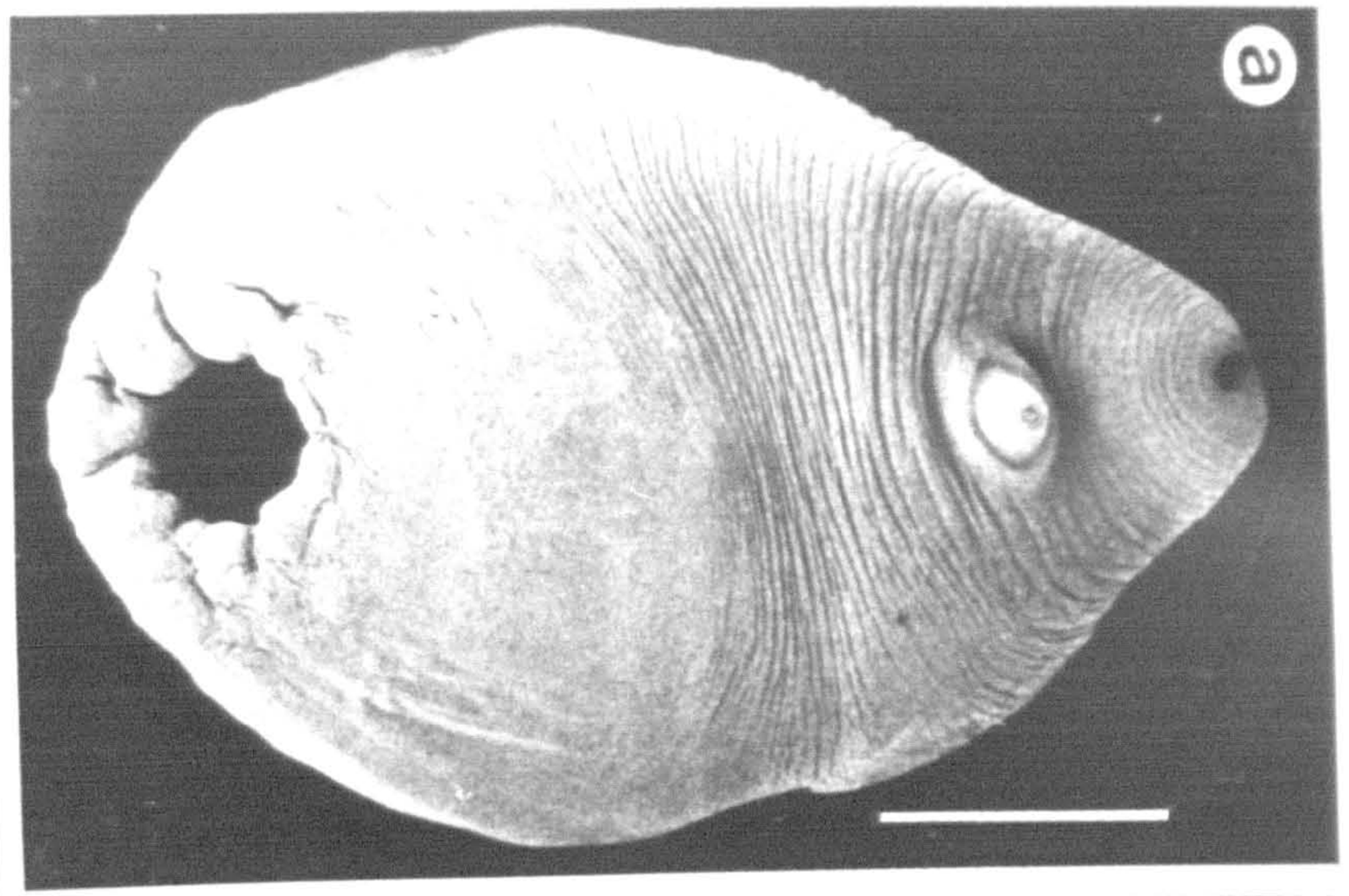
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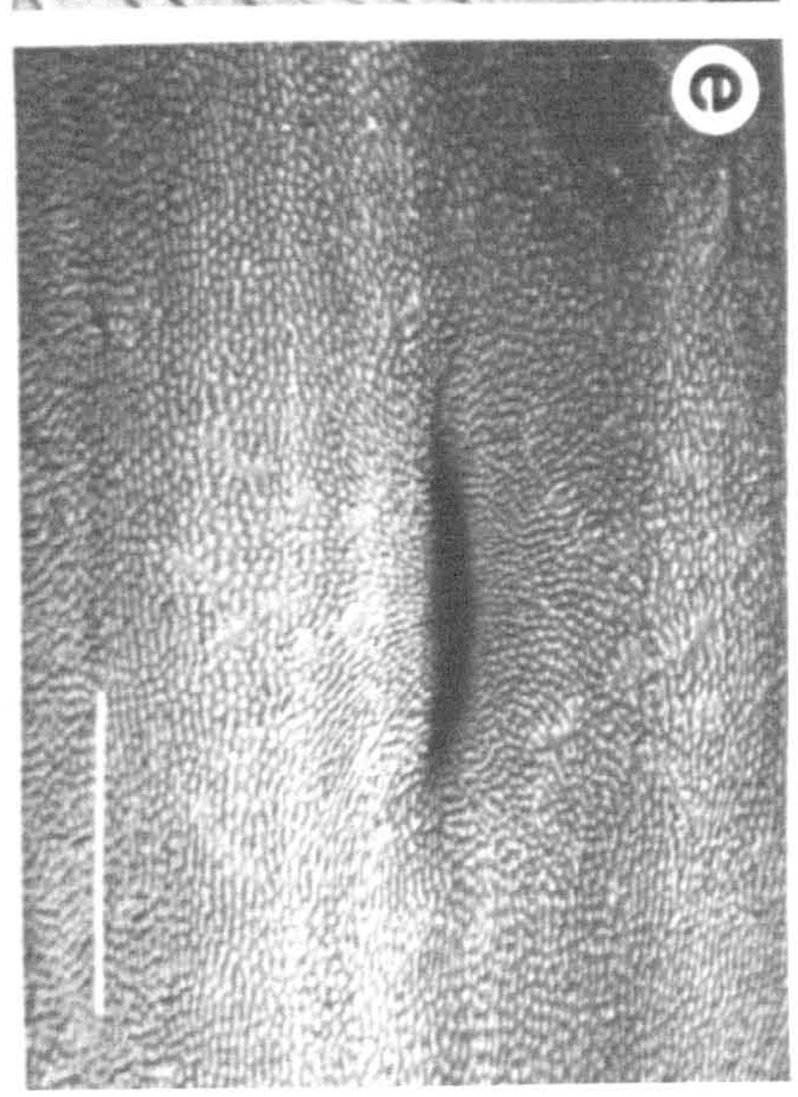
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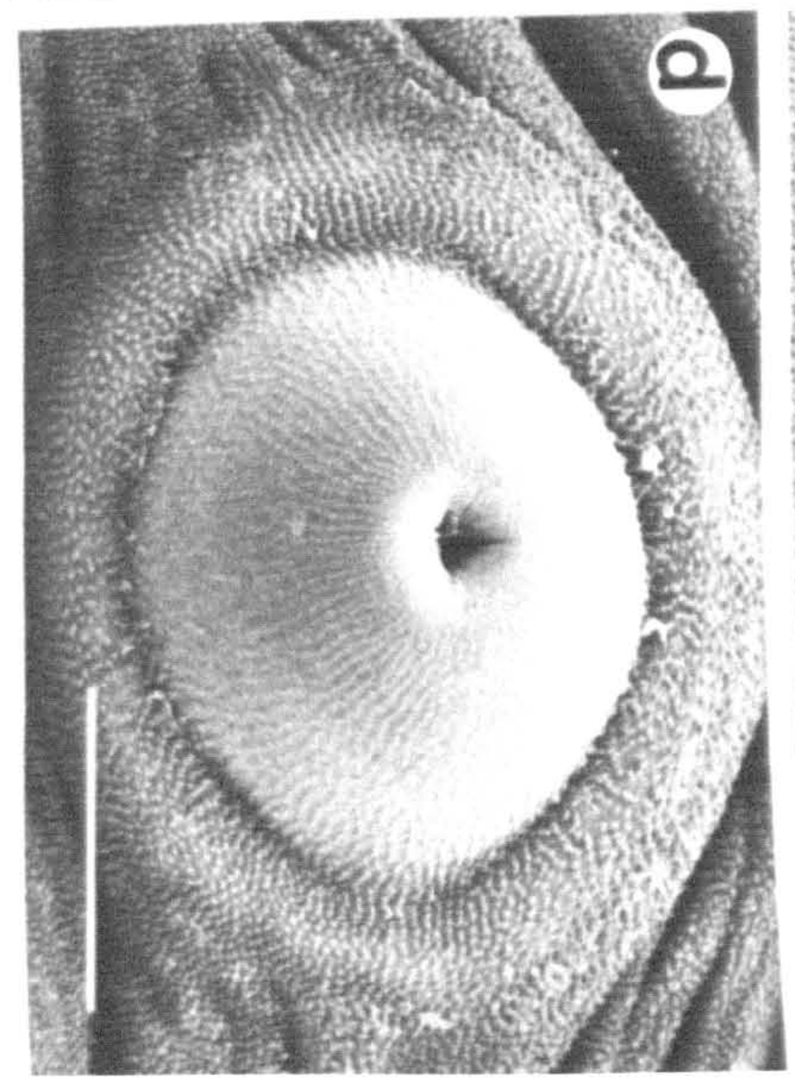
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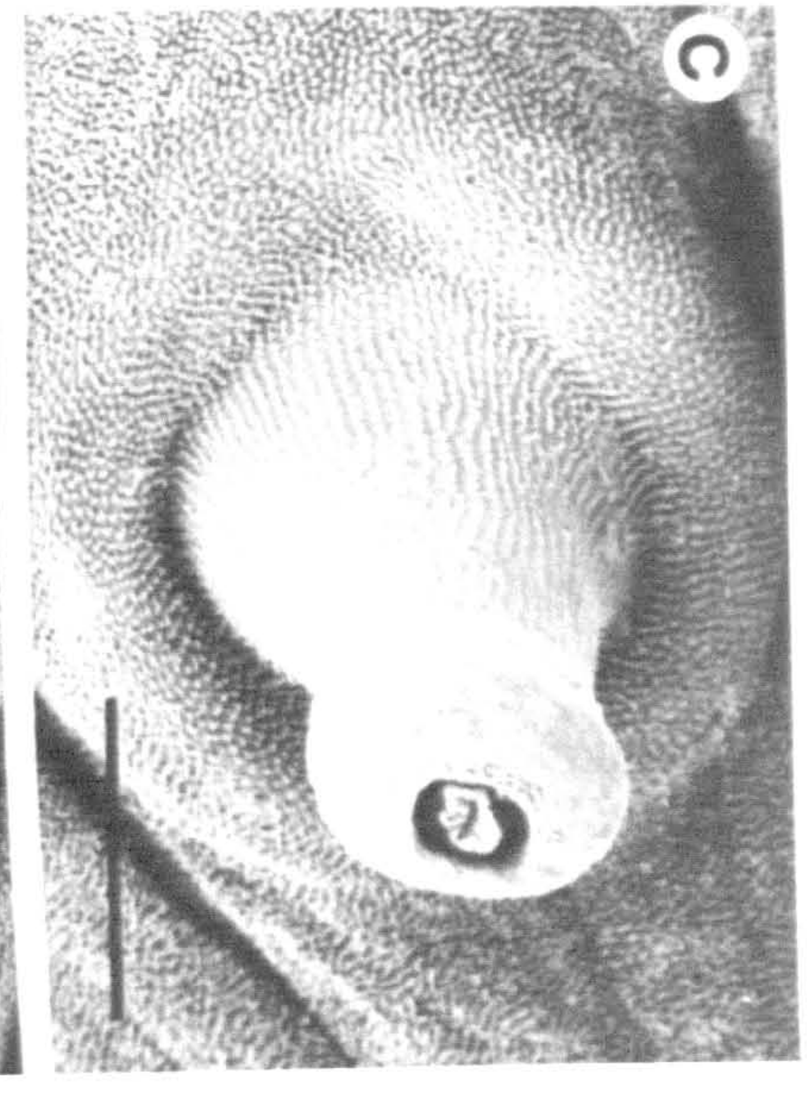

c

FIGURE 82

Calicophoron raja Näsmark, 1937

a. Whole worm, ventral view

b. Whole worm, sagittal view

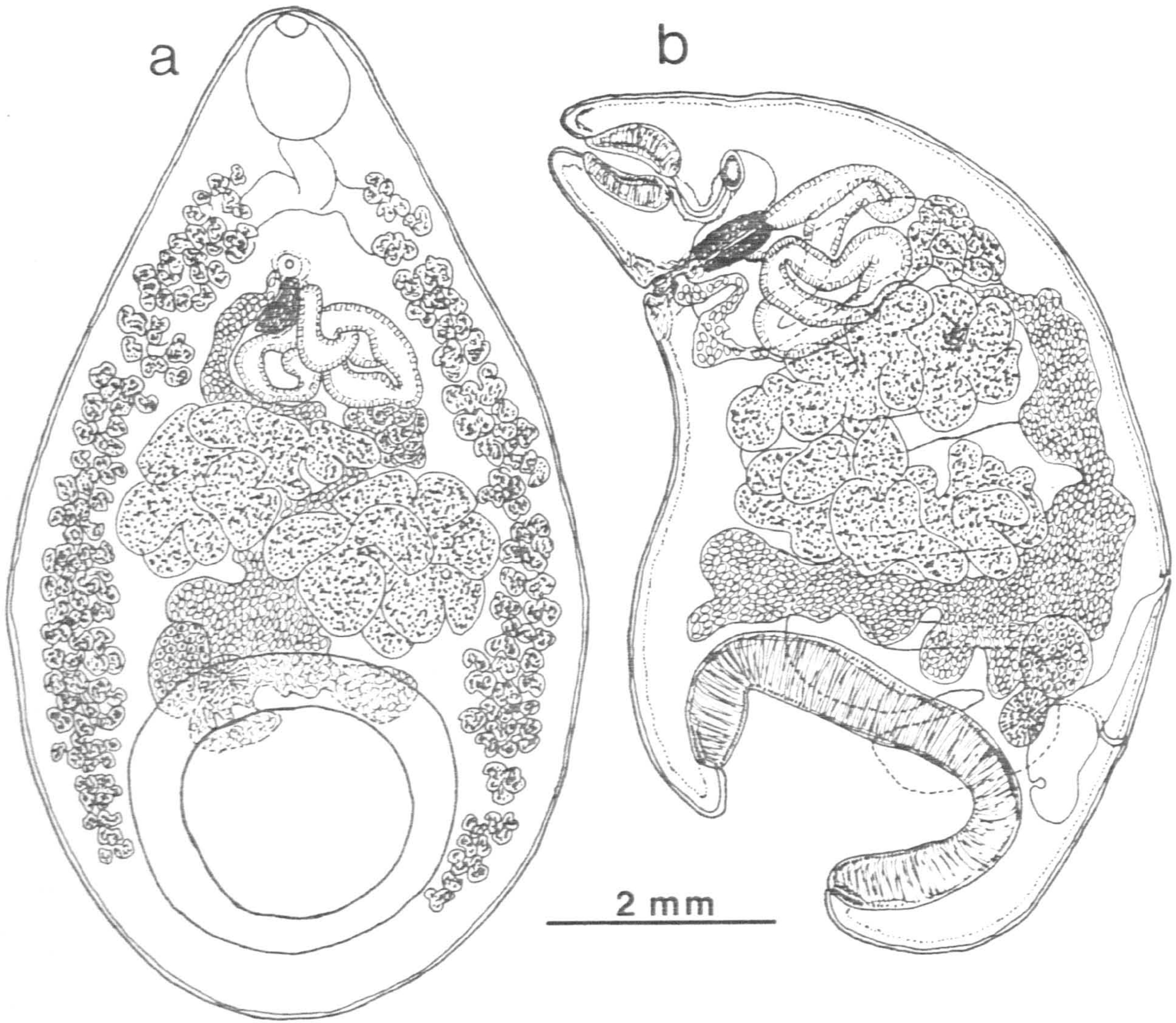

a
b
2 mm

FIGURE 83

Calicophoron räja Nasmark, 1937

(median sagittal section)

a. Acetabulum (pisum type)

b. Dorsal part of acetabulum showing the dorsal exterior circular muscle series divided into two groups of units, the second group (d.e.c.2) consists of fewer and irregularly spaced units.

c. Pharynx (calicophron type) and oesophagus

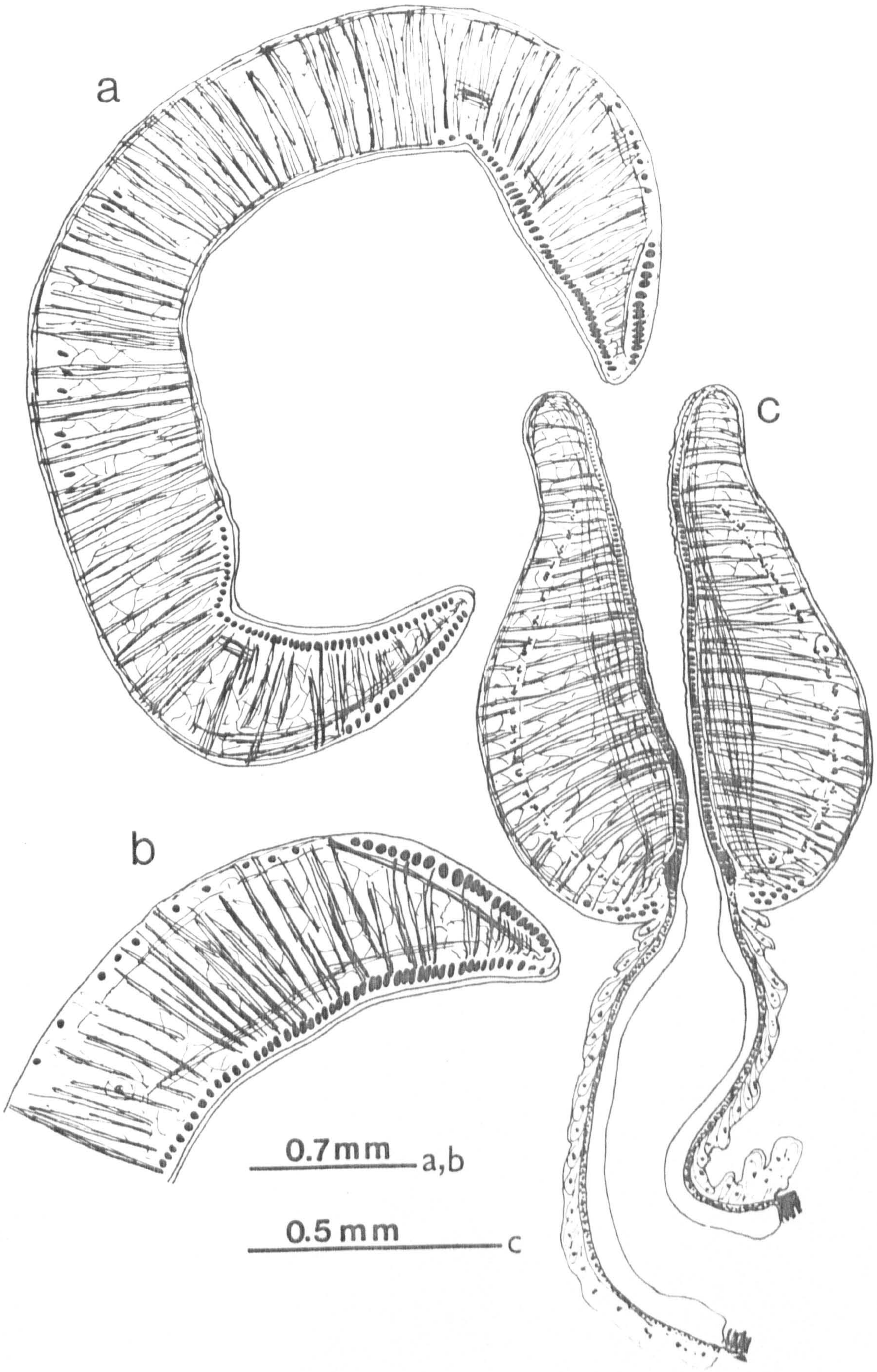

a
b
C
0.7mm
a,b
0.5mm
c

FIGURE 84

Calicophoron raja Näsmark, 1937

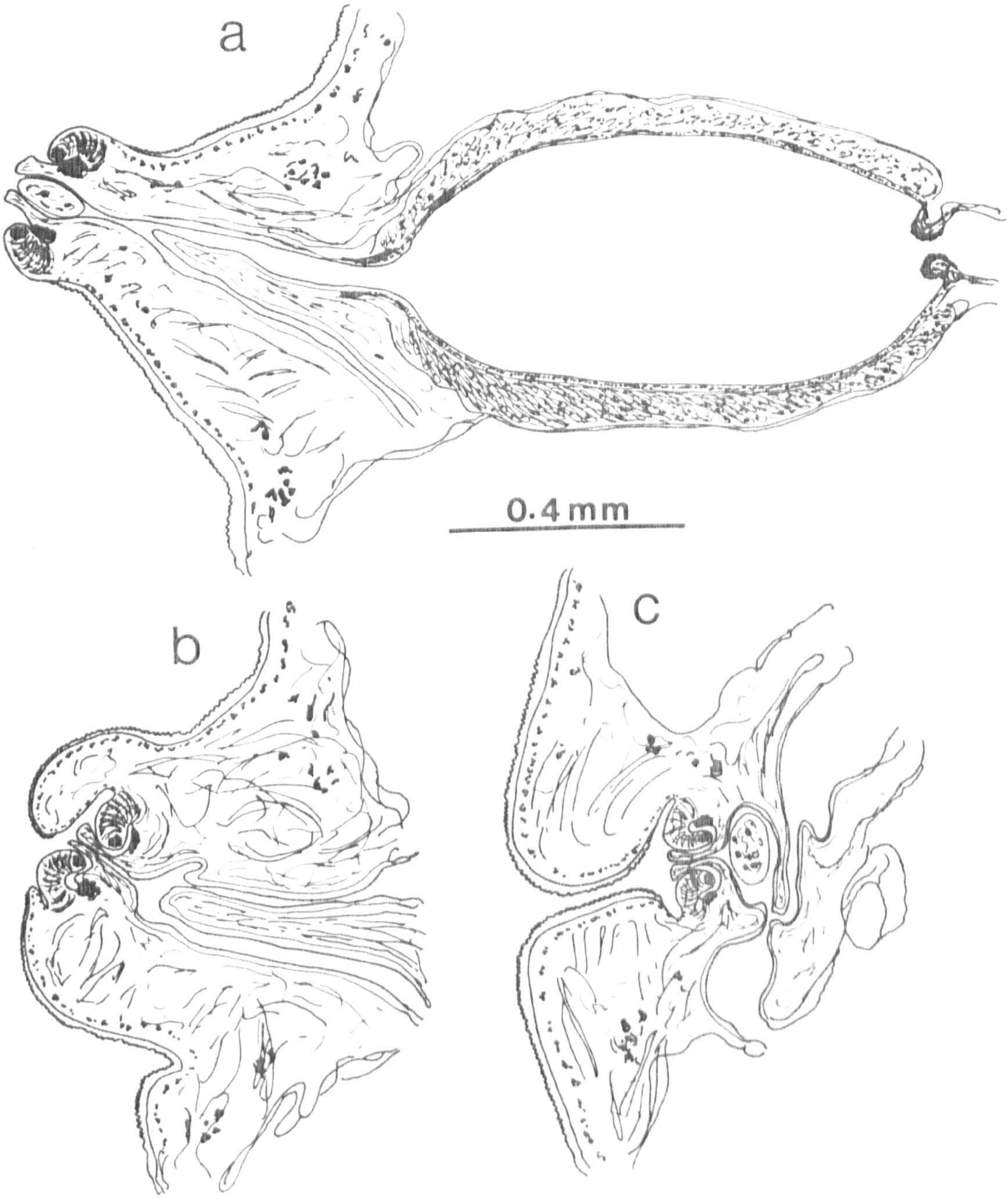
(median sagittal section)

Various forms of the terminal genitalium (raja type)

a. Fully everted genital pillar and genital papilla and showing also the pars prostatica.

b. Partly everted genital pillar

c. Fully retracted genital pillar


a
0.4 mm
b
c

Calicophoron clavula (Näsmark, 1937) n. comb.

TYPE SPECIMENS: Naturhistoriska riksmuseet, Stockholm, Sweden (RMEv Sthlm. Coll. No. JB1-5, JD1-8, I-JA1-5, I-JB1-8, II-IX-1-3, IX-1-5). From the rumen of Kobus defassa in the Sudan, stomach of Redunca redunca in the Congo (now Zaire) and Bos taurus indicus ? in Cairo, Egypt.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Aepyceros melampus	Selous Game Reserve Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Alcelaphus buselaphus	Selous Game Reserve, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Bos indicus	Mwanza, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Capra hircus	Batha, Chad	Dr. F. Bertin
Hippotragus equinus	Katagum, Nigeria	London School of Hygiene & Tropical Medicine
	Sudan	Dr. Idris
Hippotragus niger	Selous Game Reserve, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Kobus defassa harnieri	Parc National Garamba, Zaire	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Syncerus caffer	Selous Game Reserve, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Acholi, Uganda	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.

HABITAT: Rumen

DESCRIPTION:

Body conical, 4.76-8.40 mm long, 2.60-4.61 mm in the dorso-ventral direction. Body surface has dome-shaped papillae densely arranged around the oral opening and smaller ones randomly arranged and fewer in number around the acetabular opening.

Acetabulum subterminal to terminal, external diameter 1.59-2.53 mm in the dorso-ventral direction; of the paramphistomum type (sensu Näsmark, 1937) in median sagittal section; ratio to body length 1:1.9 to 1:4.7; number of circular muscle units, d.e.c.1, 13-25; d.e.c.2, 21-38; d.i.c., 40-51; v.e.c., 11-20; v.i.c., 39-60; m.e.c., 8-37. Sometimes, d.e.c.1 units are compressed together to form a sphincter.

Pharynx 0.72-1.32 mm long; 0.63-0.96 mm in the dorso-ventral direction; ratio to body length 1:5.7 to 1:8.2, to the diameter of the acetabulum 1:1.7 to 1:2.5; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section; internal surface has small dome-shaped papillae. Oesophagus 0.46-0.62 mm long, musculature of wall moderate and uniform in thickness, no bulb or posterior sphincter, lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form dorso-ventral bends, reach level of acetabulum with the blind ends directed dorsally.

Testes deeply lobed, obliquely tandem in posterior two third of the body; anterior testis 0.58-1.40 mm long, 1.06-2.40 mm in the dorso-ventral direction; posterior testis 0.63-1.80 mm long, 1.21-2.48 mm in the dorso-ventral direction; seminal vesicle thin-walled and strongly coiled; pars musculosa well developed, thick-

walled and convoluted; pars prostatica well developed, 0.30-1.00 mm long and 0.25-0.58 mm wide.

Ovary subspherical, 0.26-0.84 by 0.43-0.72 mm, posttesticular, anterior and dorsal to acetabulum on either side of the median line; Mehlis' gland immediately postero-dorsal to ovary, 0.13-0.49 by 0.15-0.72 mm; Laurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface about 0.52-2.87 mm posteriorly to the excretory pore; uterus winds forward, dorsal to testes then ventral to the male ducts; vitellaria in lateral sides, extend from level of pharynx to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 120-157 by 70.5-87 m.

Genital pore opens on the ventral surface at level of the oesophageal bifurcation or posterior to it; terminal genitalium of the clavula type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level of the posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 85

Calicophoron clavula (Näsmark, 1937) n.comb.

(SEM)

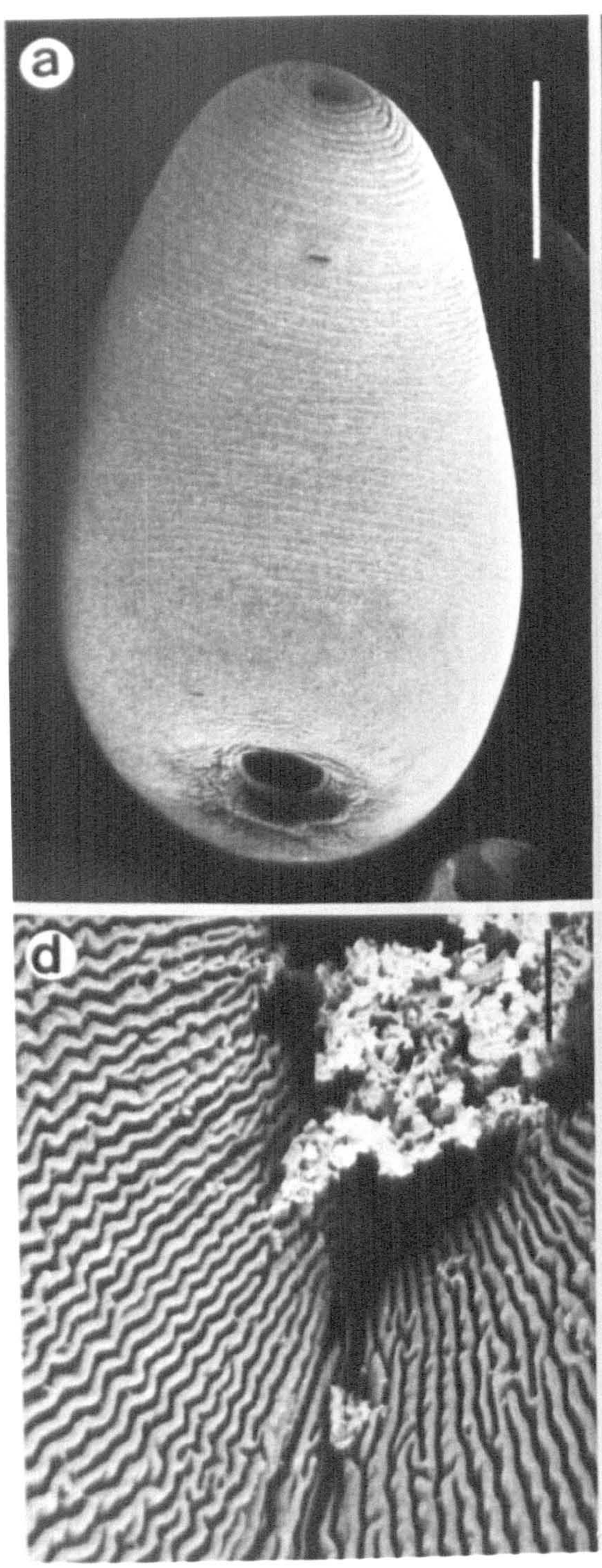
a. Whole worm, ventral view (scale bar = 2 mm)

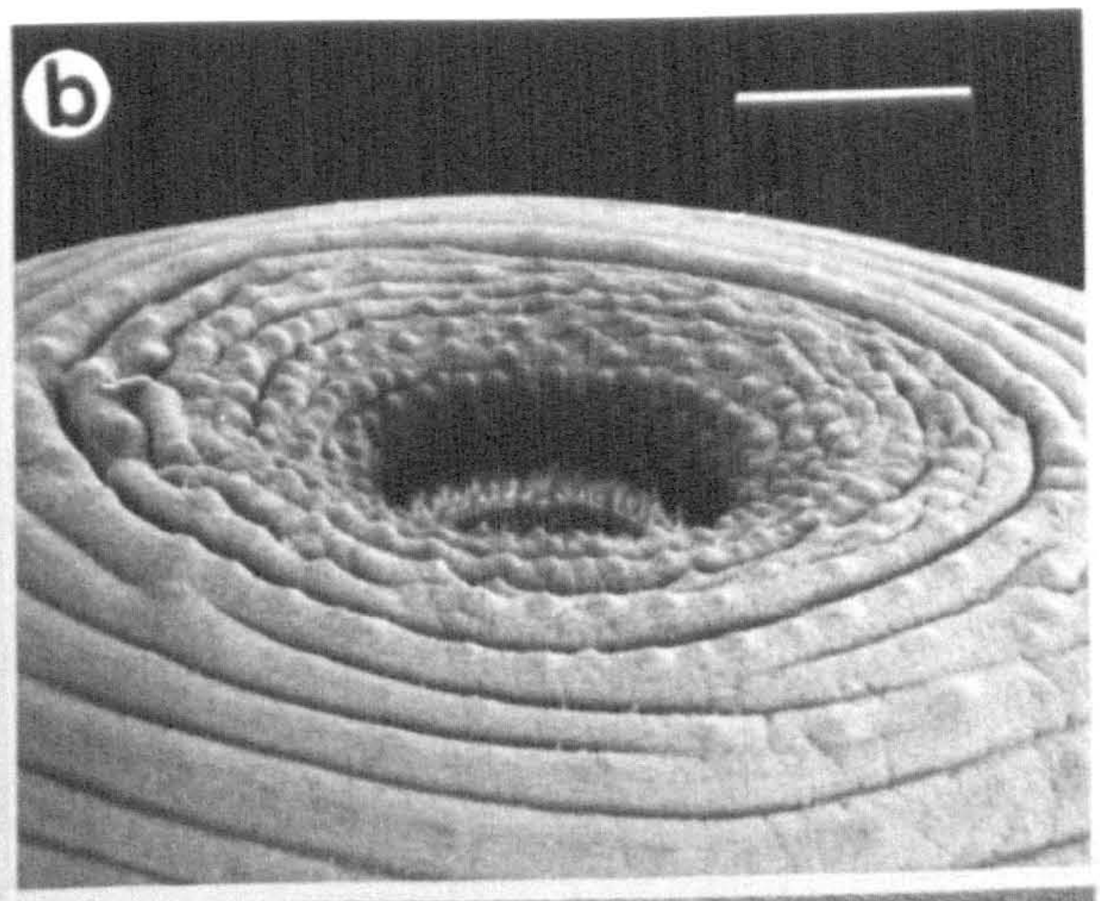
b. Anterior end, note dome-shaped papillae around oral opening (scale bar = 200 µm)

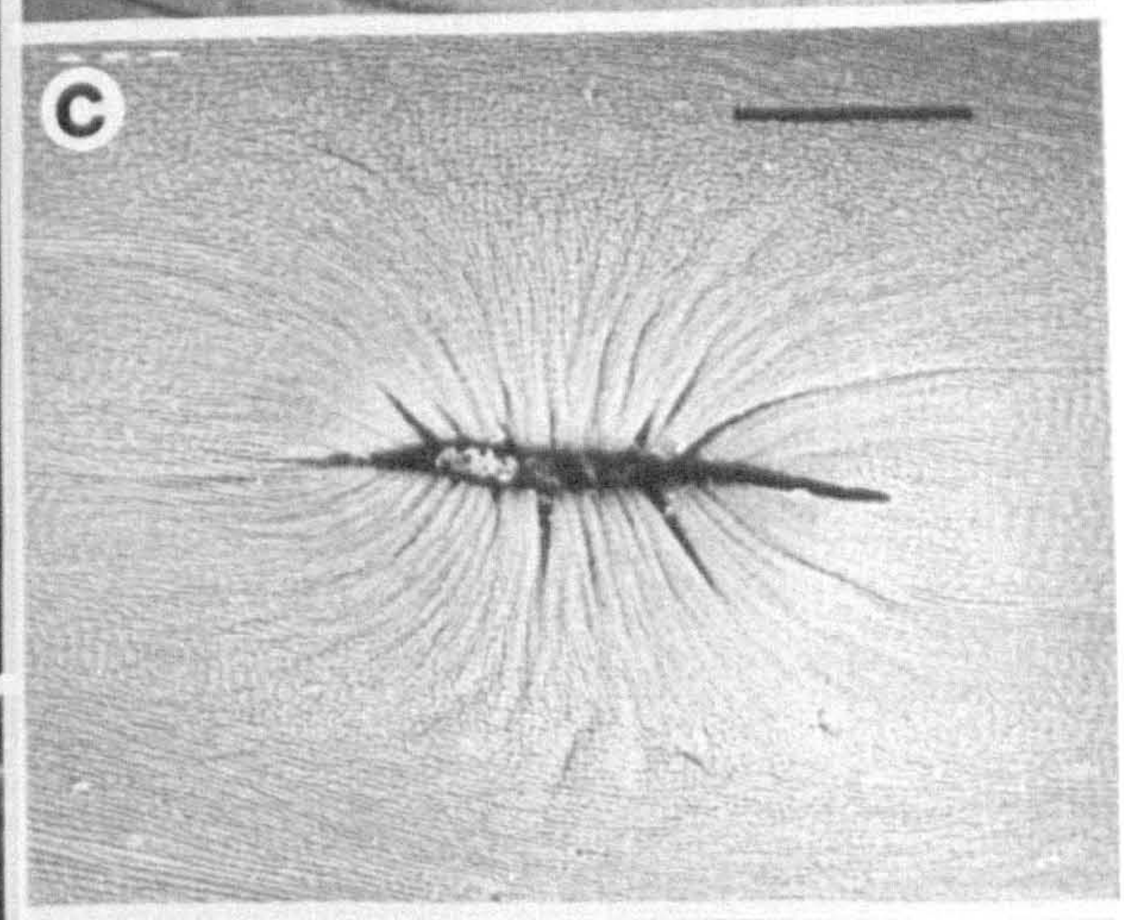
c. Genital pore region (scale bar = 100 µm)

d. Closer view of part of genital pore wall showing fine ridges (scale bar = 10 µm)

e. Acetabular region, note presence of much smaller, fewer and randomly arranged papillae (scale bar = 600 µm)


a


b


c

d

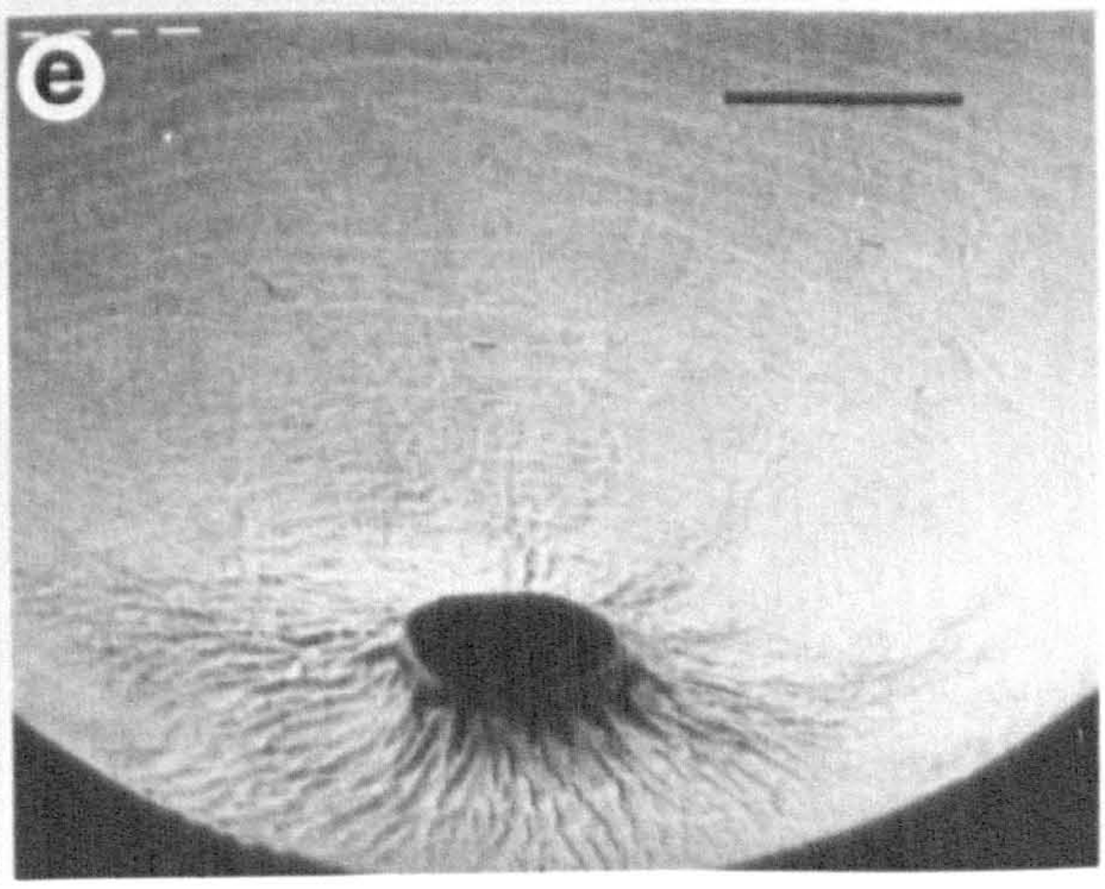

e

FIGURE 86

Calicophoron clavula (Näsmark, 1937) n. comb.

a. Whole worm, ventral view

b. Whole worm, sagittal view

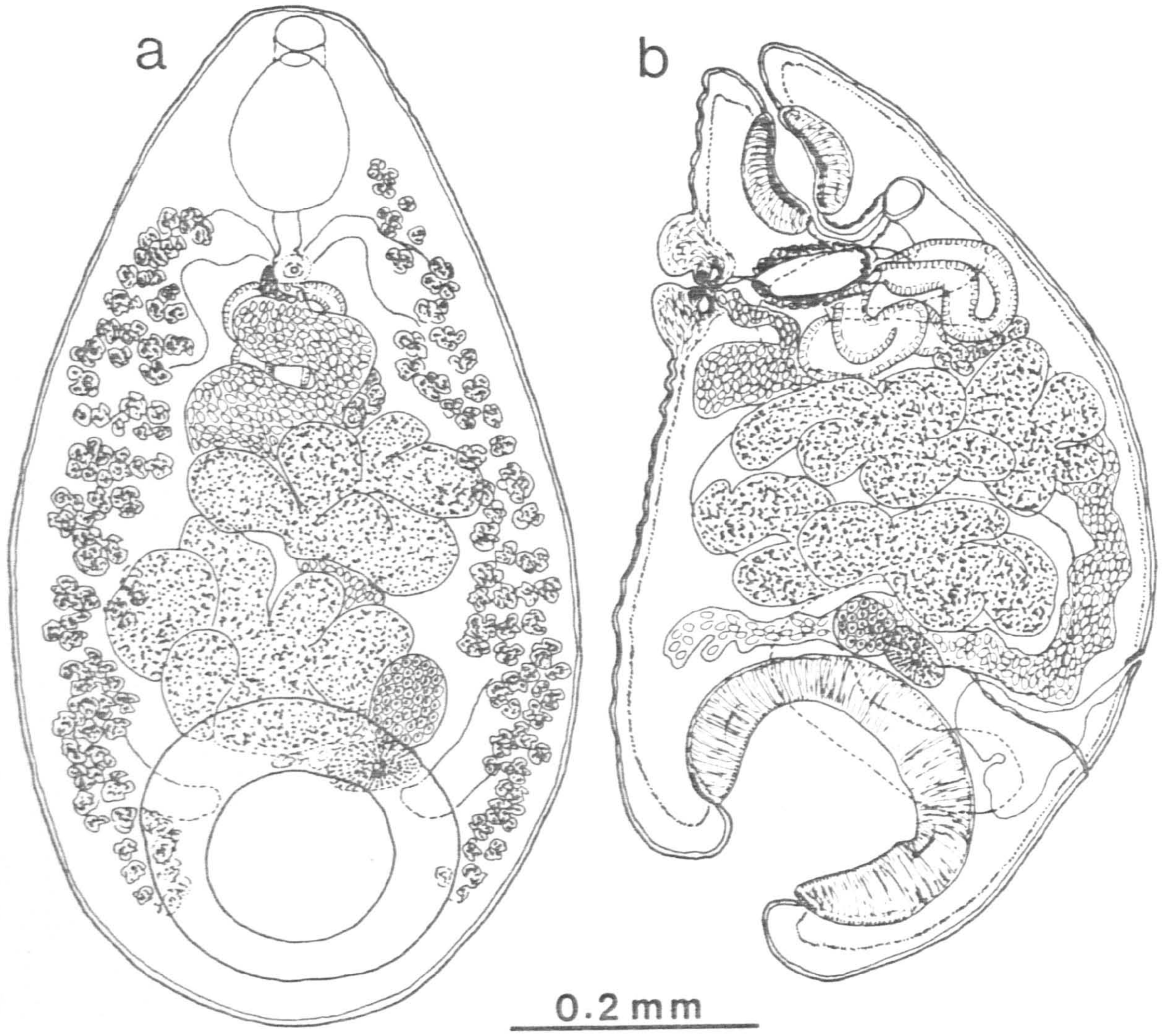

a
b
0.2 mm

FIGURE 87

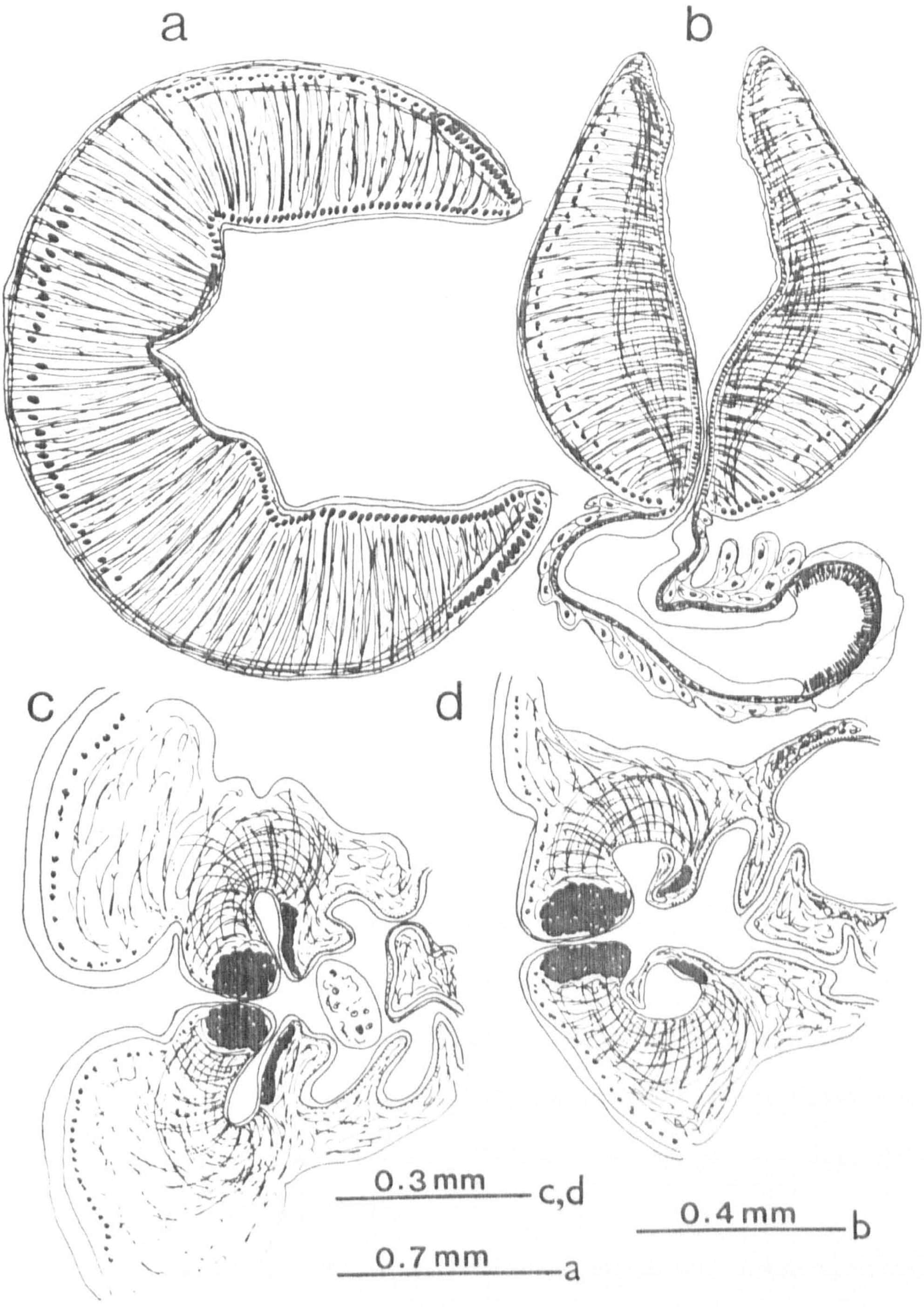
Calicophoron clavula (Näsmark, 1937) n. comb.
(median sagittal section)

a. Acetabulum (paramphistomum type)

b. Pharynx (calicophoron type) and oesophagus

c. Terminal genitalium (clavula type), retracted form

d. Terminal genitalium (clavula type), normally relaxed form


a
b
c
d
0.3 mm
c,d
0.7 mm
a
0.4 mm
b

Calicophoron microbothrioides (Price and McIntosh, 1944) n. comb.

Synonym: Ceylonocotyle petrovi Davydova, 1961

TYPE SPECIMENS: United States National Parasite Collection, USDA, Beltsville, Maryland (USNMH Coll. Nos. 45699 & 18424), from the rumen of Bos taurus in Wichita, Kansas, U.S.A.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos taurus	Cuba	Dr. J. Prokopič
	Puerto Rico	Dr. Delfin de Leon. Material labeled "Cotylophoron cotylophorum".
	Georgia, U.S.A.	Dr. A.K, Prestwood

HABITAT: Rumen

DESCRIPTION:

Body conical, 4.50-6.80 mm long, 1.80-2.50 mm in the dorso-ventral direction. Body surface has papillae present on the anterior end around the oral opening and ventrally around the genital pore region. Those on the former are much smaller than those on the latter.

Acetabulum subterminal, external diameter 1.13-1.81 mm in the dorso-ventral direction; ratio to body length 1:3.1 to 1:4.8; of the pisum type (sensu Näsmark, 1937) in median sagittal section with the d.e.c.2 units irregularly spaced; number of circular muscle units, d.e.c.1, 14-19; d.e.c.2, 2-12; d.i.c., 34-43; v.e.c., 12-16; v.i.c., 32-48; m.e.c., 15-23.

Pharynx 0.40-0.68 mm long, 0.30-0.59 mm in the dorso-ventral direction; ratio to body length 1:8.2 to 1:11.5, to the diameter of the acetabulum 1:2 to 1:2.6; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section; internal surface has small dome-

shaped papillae. Oesophagus 0.22-0.88 mm long, musculature of wall expanded into a bulb in its posterior part, lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form dorso-ventral bends, reach level of acetabulum with the blind ends directed dorsally.

Testes lobed, directly or obliquely tandem in posterior two third of the body; anterior testis 0.50-0.98 mm long, 1.23-1.83 mm in the dorso-ventral direction; posterior testis 0.58-1.08 mm long, 1.21-1.80 mm in the dorso-ventral direction; seminal vesicle deeply coiled and thin-walled; pars musculosa well developed, thick-walled and convoluted; pars prostatica well develoed, 0.21-0.37 mm long and 0.20-0.29 mm wide.

Ovary subspherical, 0.30-0.52 by 0.37-0.72 mm, posttesticular and antero-dorsal to ovary and Mehlis' gland; Mehlis' gland close to ovary, 0.23-0.35 by 0.25-0.41 mm; Laurer's canal crosses excretory vesicle or duct and opens on the dorsal surface about 0.35-0.56 mm posteriorly to the excretory pore; uterus winds forward dorsal to testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of oesophagus to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 114-13o by 67.5-75 µm.

Genital pore opens on the ventral surface at level posterior to the oesophageal bifurcation, encircled by an oval or round swelling; terminal genitalium of the microbothrium type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level of the female glands and anteriorly to the Laurer's canal opening.

FIGURE 88

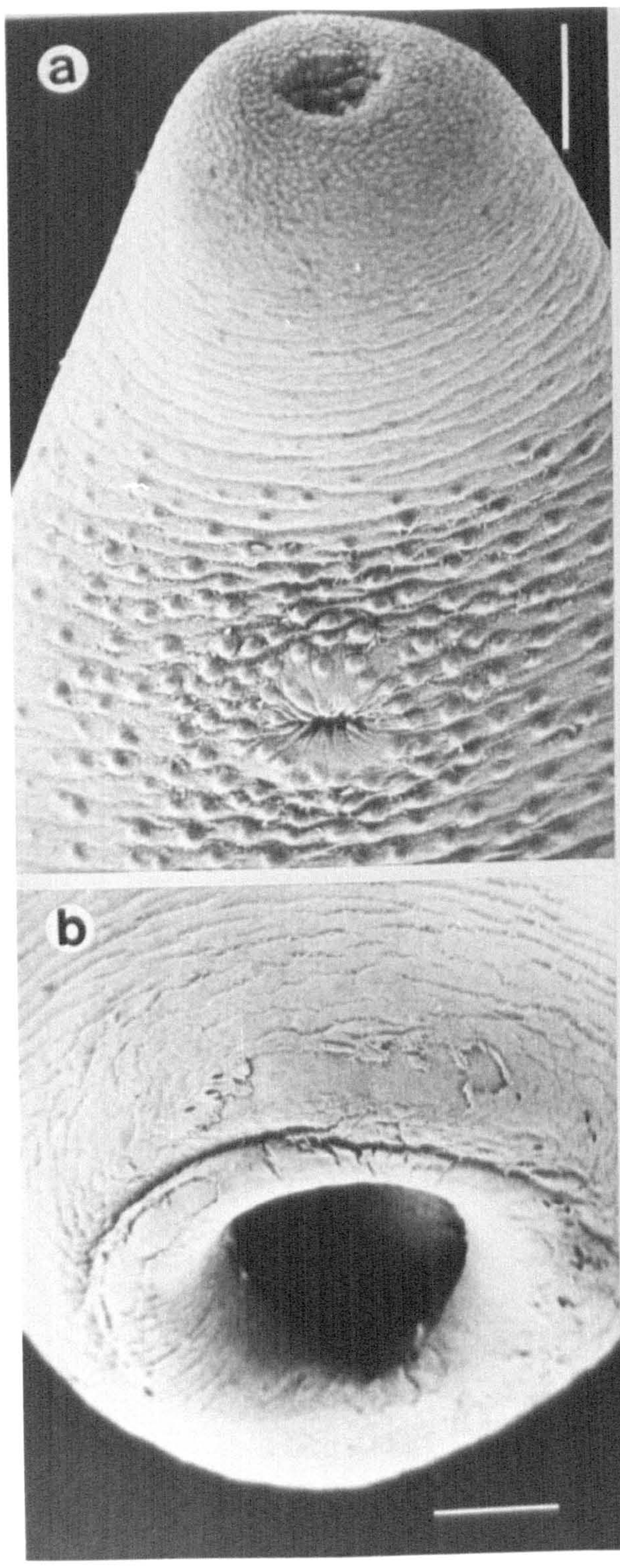
Calicophoron microbothrioides (Price and McIntosh, 1944) n. comb.
(SEM)

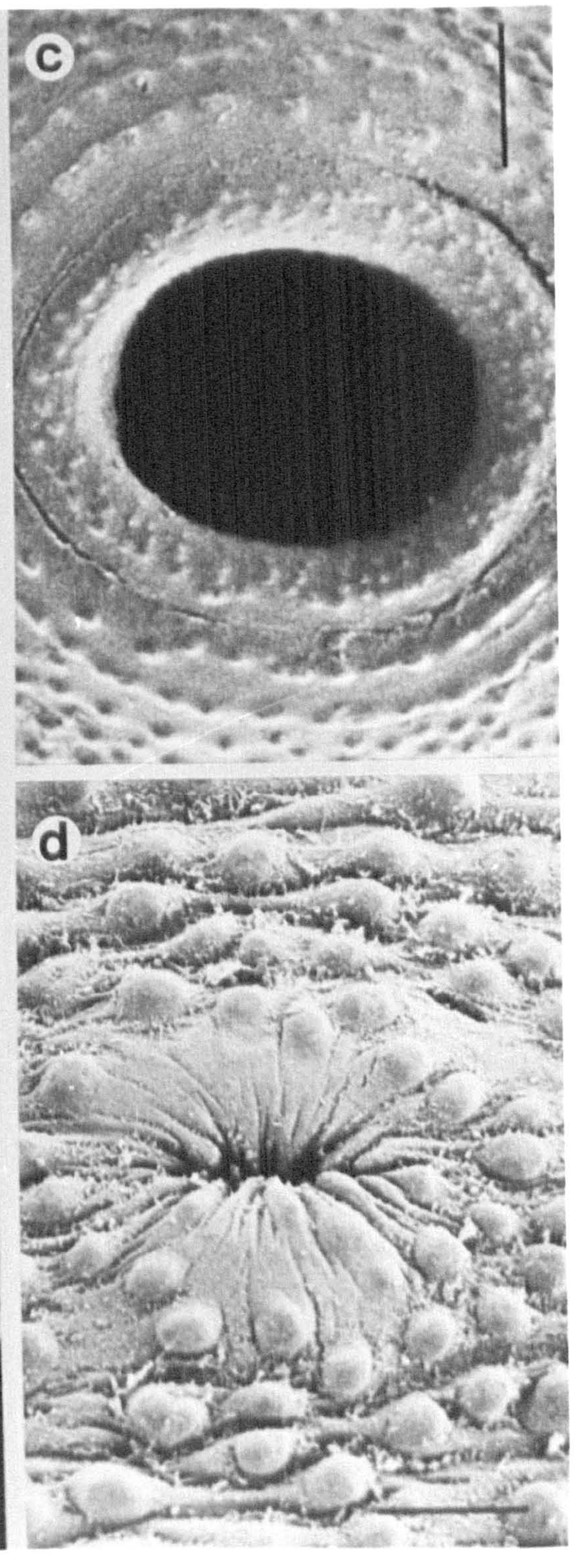
a. Anterior part of worm, ventral view. Note larger papillae around genital pore region and smaller ones around the oral end (scale bar = 200 µm).

b. Acetabular region (scale bar = 200 µm)

c. Oral end showing arragement of papillae (scale bar = 100 µm)

d. Genital pore region, note large and dome-shaped papillae (scale bar = 100 µm)


a


c

b

d

FIGURE 89

Calicophoron microbothrioides (Price and McIntosh, 1944) n. comb.

a. Whole worm, ventral view

b. Whole worm, sagittal view

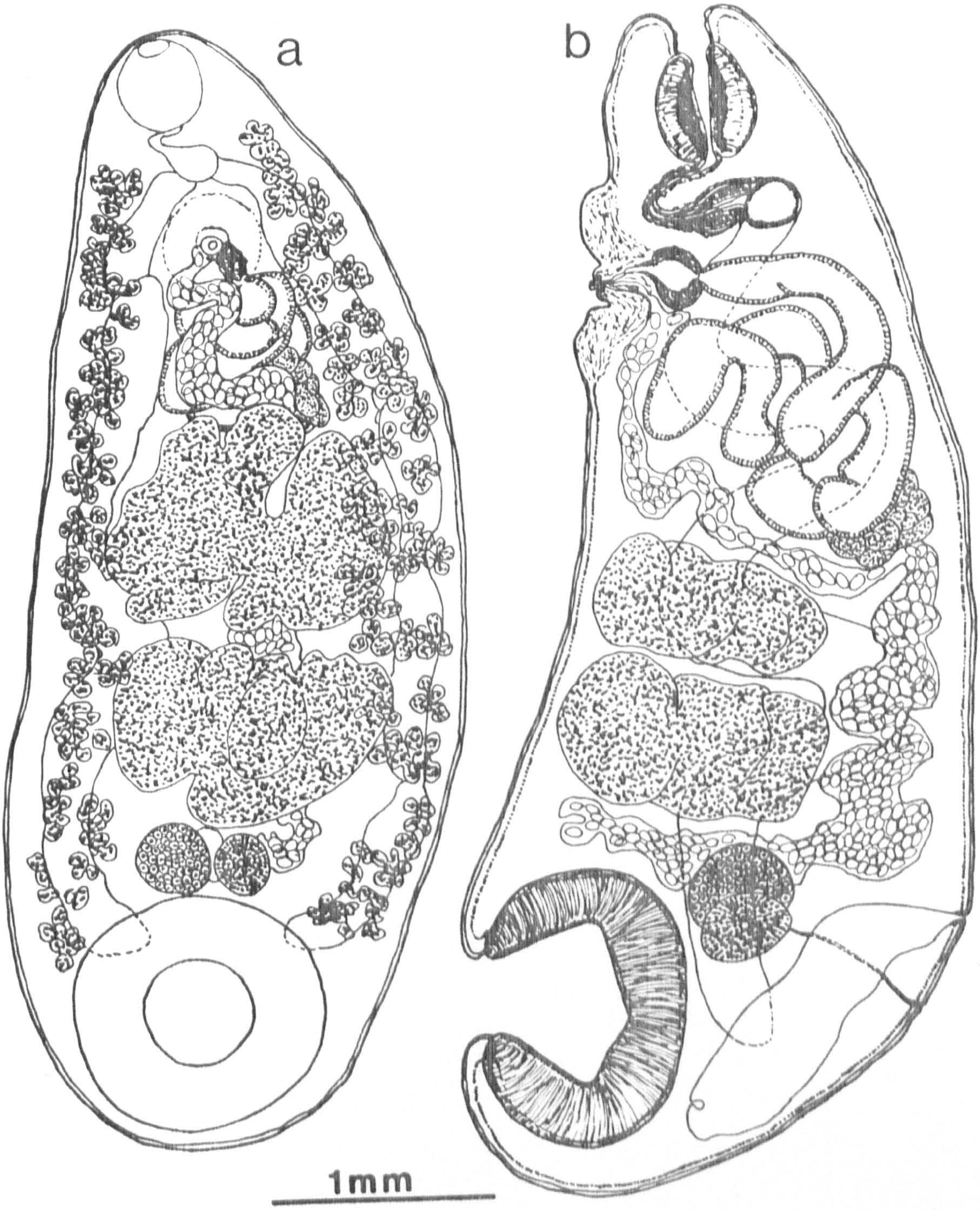

a
b
1mm

FIGURE 90

Calicophoron microbothrioides (Price and McIntosh, 1944) n. comb.

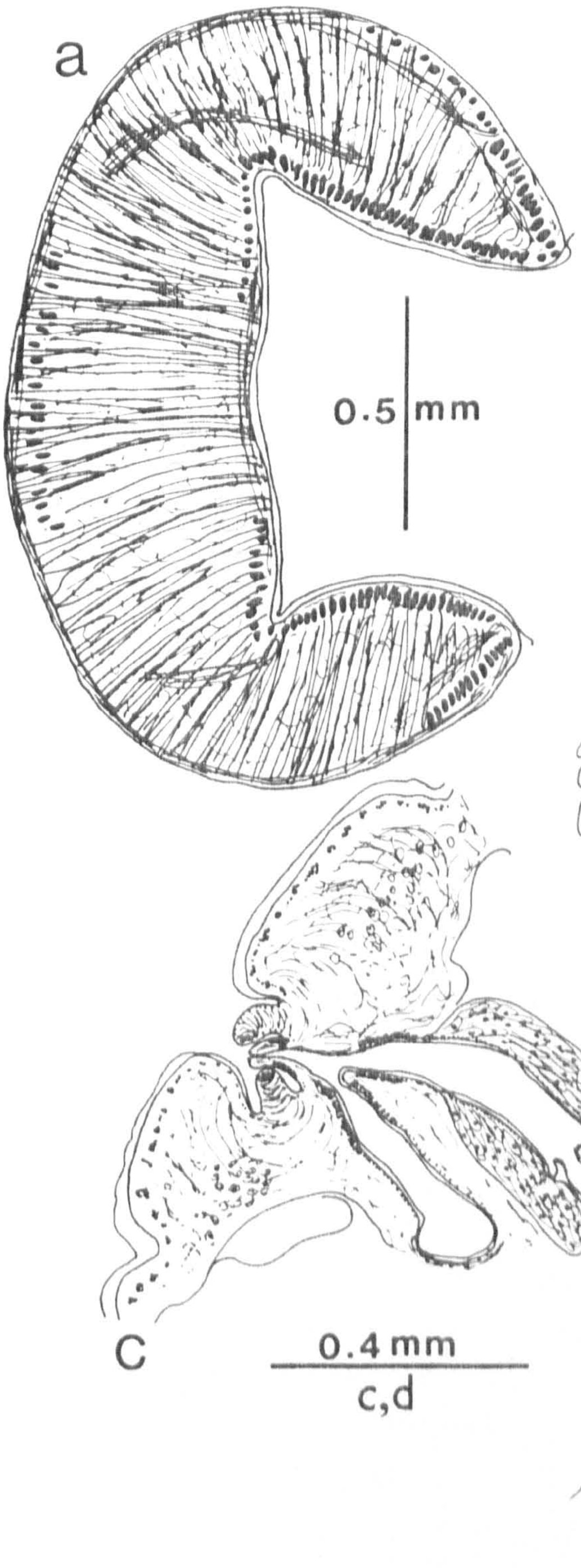
(median sagittal section)

a. Acetabulum (pisum type)

b. Pharynx (calicophoron type) and oesophagus. Note presence of oesophageal bulb.

c. Terminal genitalium (microbothrium type), retracted form and pars prostatica

d. Terminal genitalium (microbothrium type), relaxed form


a
0.5 mm
b
0.3 mm
C
0.4 mm
c,d
d

Calicophoron sukari (Dinnik, 1954) n. comb.

TYPE SPECIMENS: British Museum (Natural History) Helminth Collection Number 1961.8.16.50-106, from the reticulum of Bos taurus in Sukari Farm, Nairobi, Kenya.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos indicus	Musoma, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Bos taurus	Nairobi Abattoir, Kenya	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Cattle	Ethiopia	London School of Hygiene & Tropical Medicine
	Mwanza, Tanzania	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
	Uganda	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Lochinvar, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Sheep	Ethiopia	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Syncerus caffer	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.

HABITAT: Rumen and Reticulum

DESCRIPTION:

Body conical 6.00-9.28 mm long, 1.60-3.68 mm in the dorso-ventral direction. Body surface has papillae present around the oral opening, ventrally around the genital pore region and around the acetabular opening. Those on the oral end are smaller than those on the genital pore region and those around the acetabular opening are much smaller, fewer and randomly arranged than those on the first two.

Acetabulum subterminal, 1.30-1.68 mm in external diameter in the dorso-ventral direction; ratio to body length 1:4 to 1:6.3; of the calicophoron type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 11-18; d.i.c., 30-42; v.e.c., 11-16; v.i.c., 29-45; m.e.c., 5-8.

Pharynx 0.55-0.80 mm long, 0.60-0.68 mm in the dorso-ventral direction; ratio to body length 1:10 to 1:14, to the diameter of the acetabulum 1:1.8 to 1:2.7; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section); internal surface has small dome-shaped papillae. Oesophagus 0.55-0.88 mm long, musculature of wall moderate and uniform in thickness, no bulb or posterior sphincter; lumen has two types of lining, anterior one third lined by hyaline layer while the posterior two third lined by ciliated epithelium same as that found lining the caeca. Caeca in lateral sides of the body, form dorso-ventral bends, reach level of acetabulum with the blind ends directed ventrally.

Testes deeply lobed, directly tandem in posterior two third of the body; anterior testis 0.60-1.40 mm long, 1.21-2.42 mm in the dorso-ventral direction; posterior testis 1.52-1.60 mm long,

1.48-2.40 mm in the dorso-ventral direction; seminal vesicle thin-walled and coiled; pars musculosa well developed, thick-walled and convoluted; pars prostatica well developed, 0.31-0.40 mm long and 0.28-0.29 mm wide.

Ovary subspherical, 0.27-0.68 by 0.46-0.73 mm, posttesticular and anterior to acetabulum; Mehlis' gland close to ovary, 0.25-0.45 by 0.35-0.62 mm; uterus winds forward dorsal to testes then ventral to the male ducts; Laurer's canal crosses excretory vesicle or duct and opens on the dorsal surface about 0.25-0.65 mm posteriorly to the excretory pore; vitellaria in lateral fields, extend from level of oesophagus to acetabulum, confluent dorso-medially in their anterior limits; egg 137-165 by 71-92 µm.

Genital pore opens on ventral surface at level posterior to the oesophageal bifurcation. Terminal genitalium of the micro-bothrium type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level of posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 91

Calicophoron sukari (Dinnik, 1954) n. comb.

(SEM)

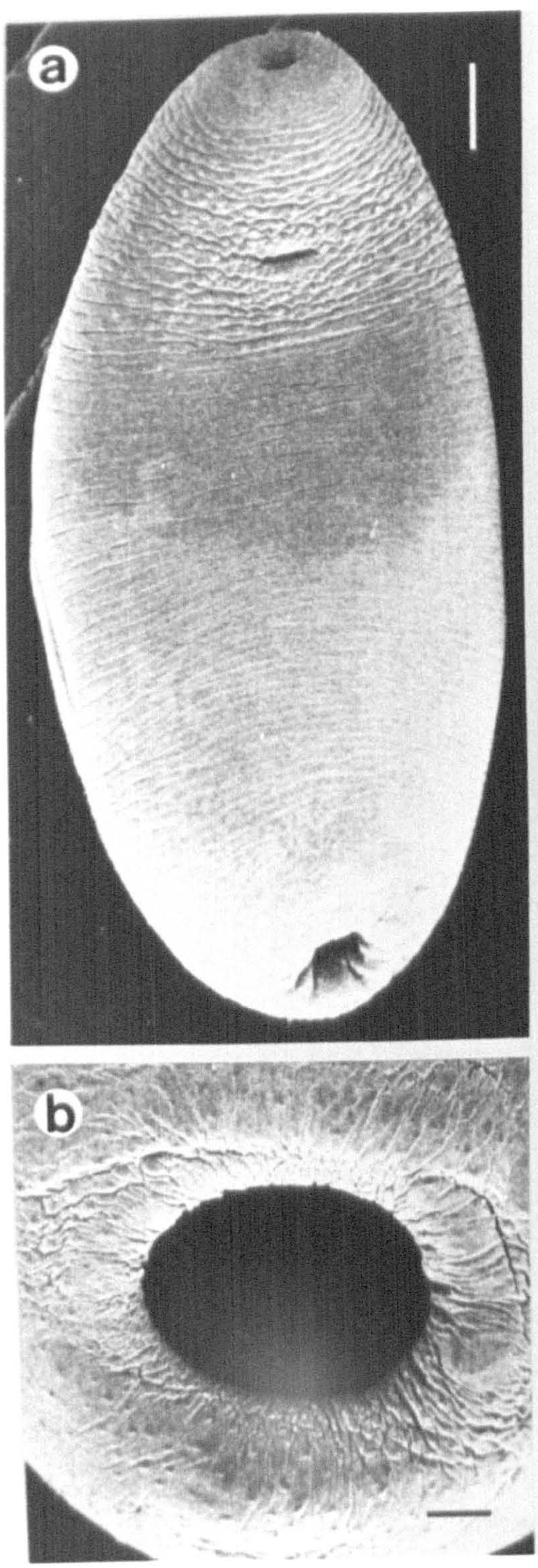
a. Whole worm, ventral view (scale bar = 500 µm)

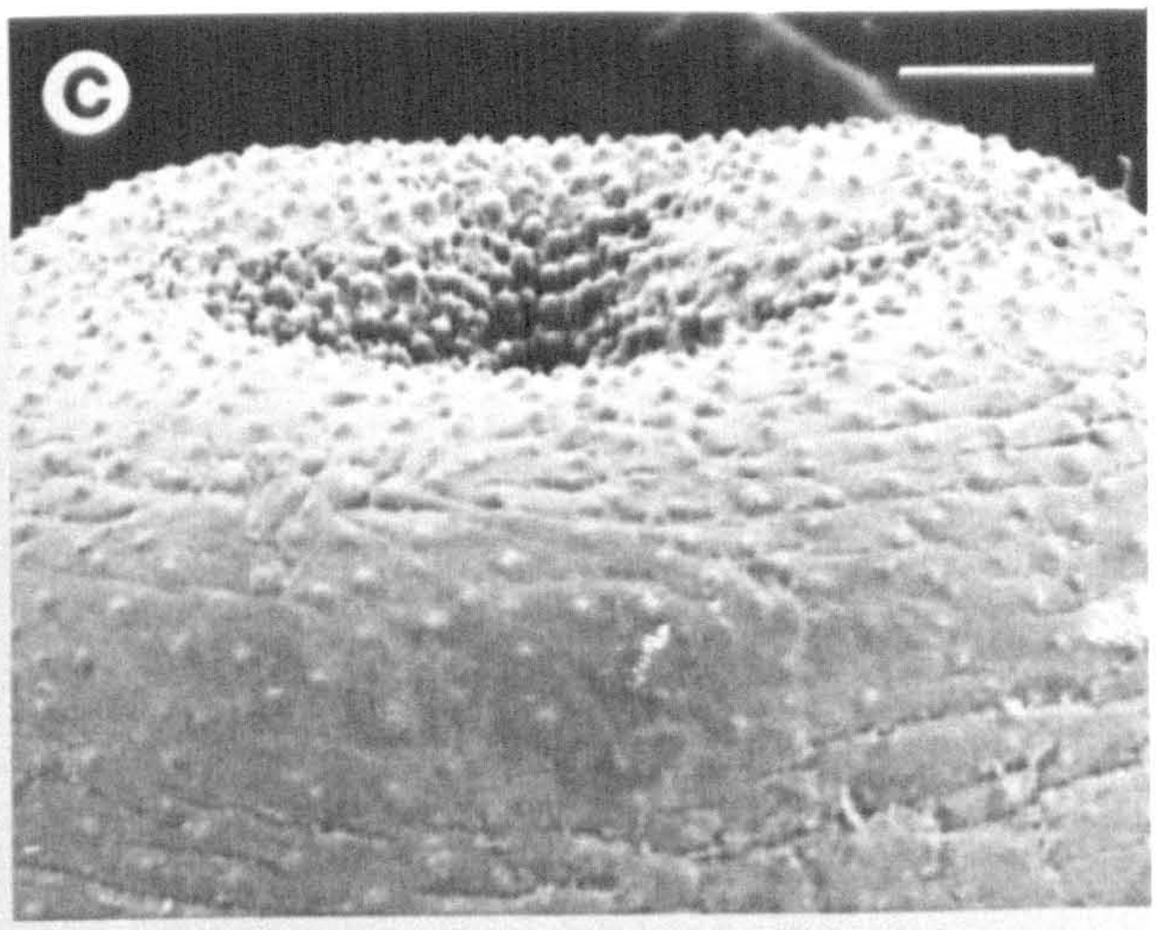
b. Acetabular region, note presence of small, few and randomly arranged papillae (scale bar = 100 µm)

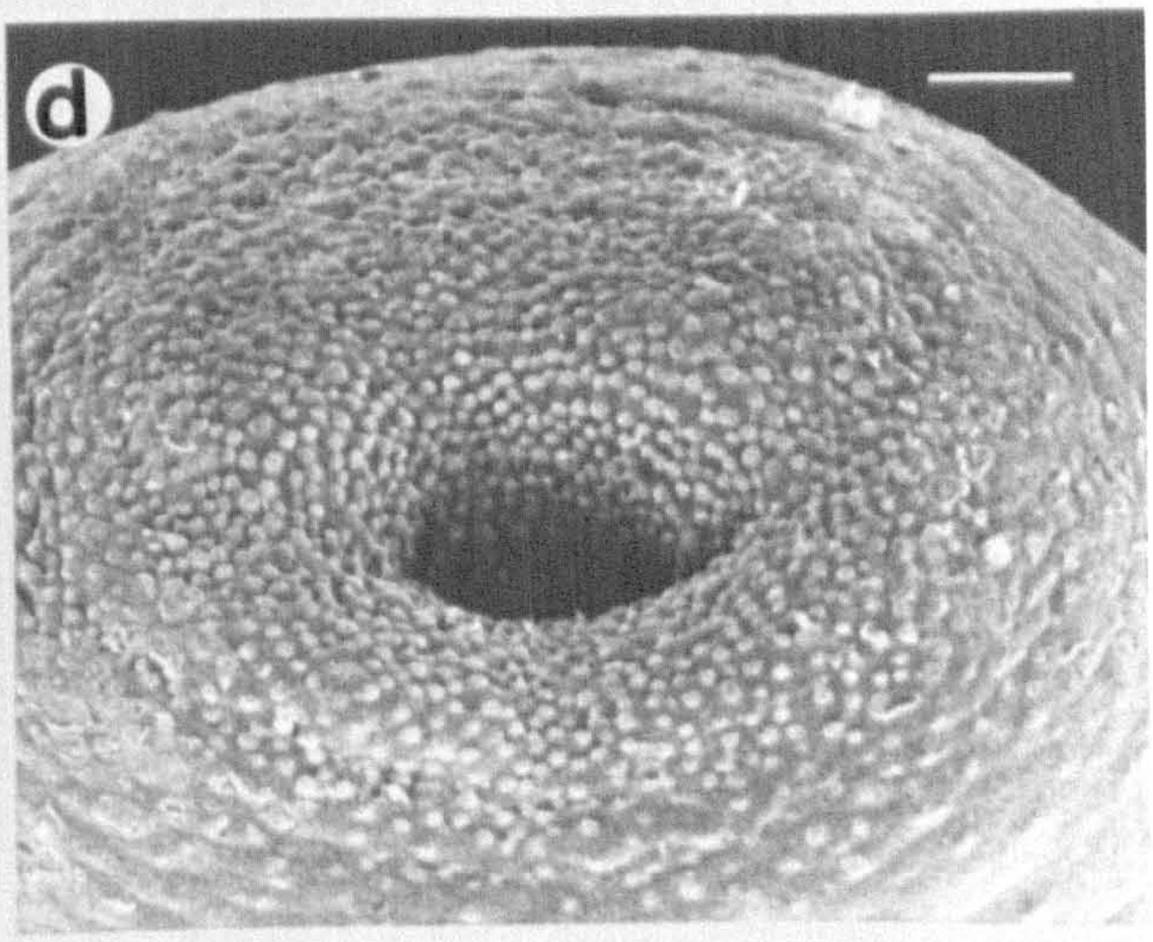
c. Anterior end showing small papillae (scale bar = 100 µm)

d. Another anterior end showing arrangement of papillae around oral opening (scale bar = 100 µm)

e. Genital pore region, note presence of dome-shaped papillae which are larger than those on the anterior end and acetabular region (scale bar = 100 µm)


a


c


d

b

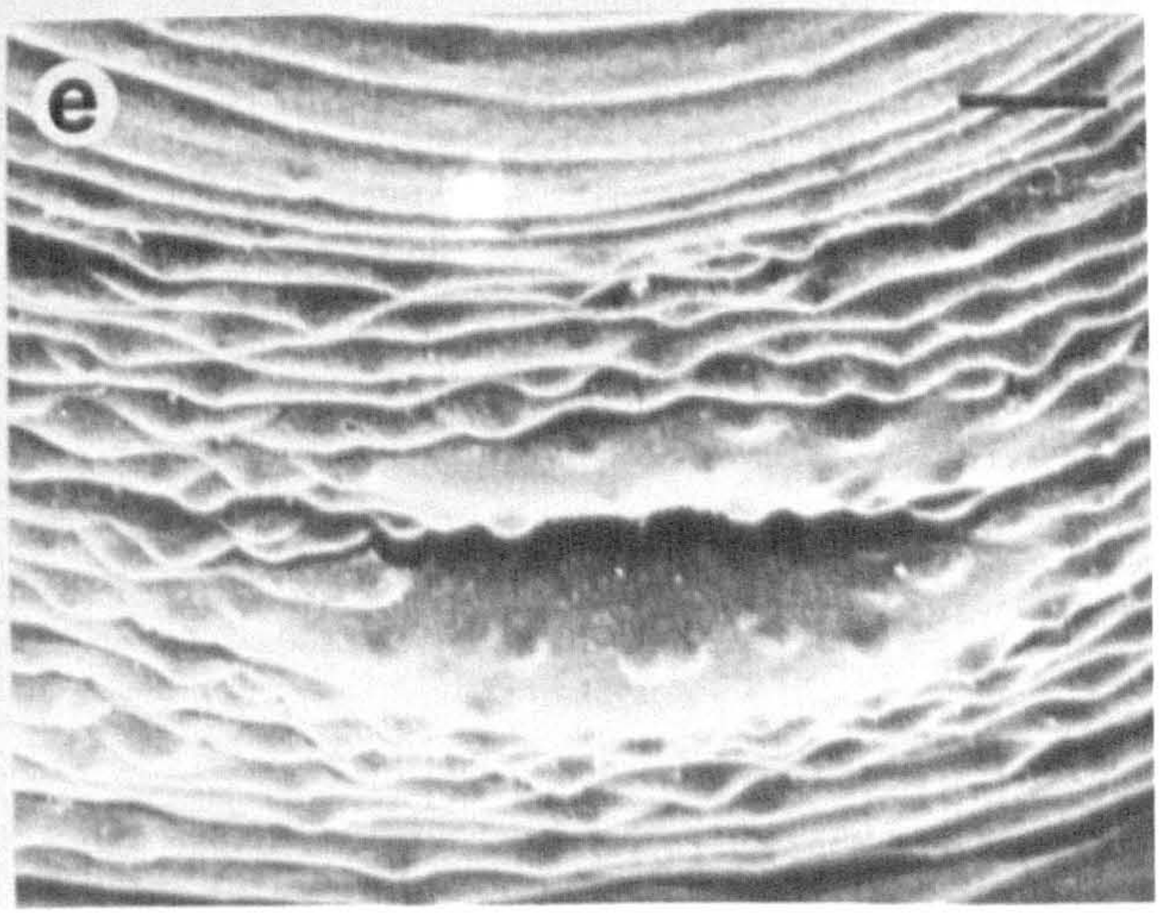

e

FIGURE 92

Calicophoron sukari (Dinnik, 1954) n. comb.

a. Whole worm, ventral view

b. Whole worm, sagittal view

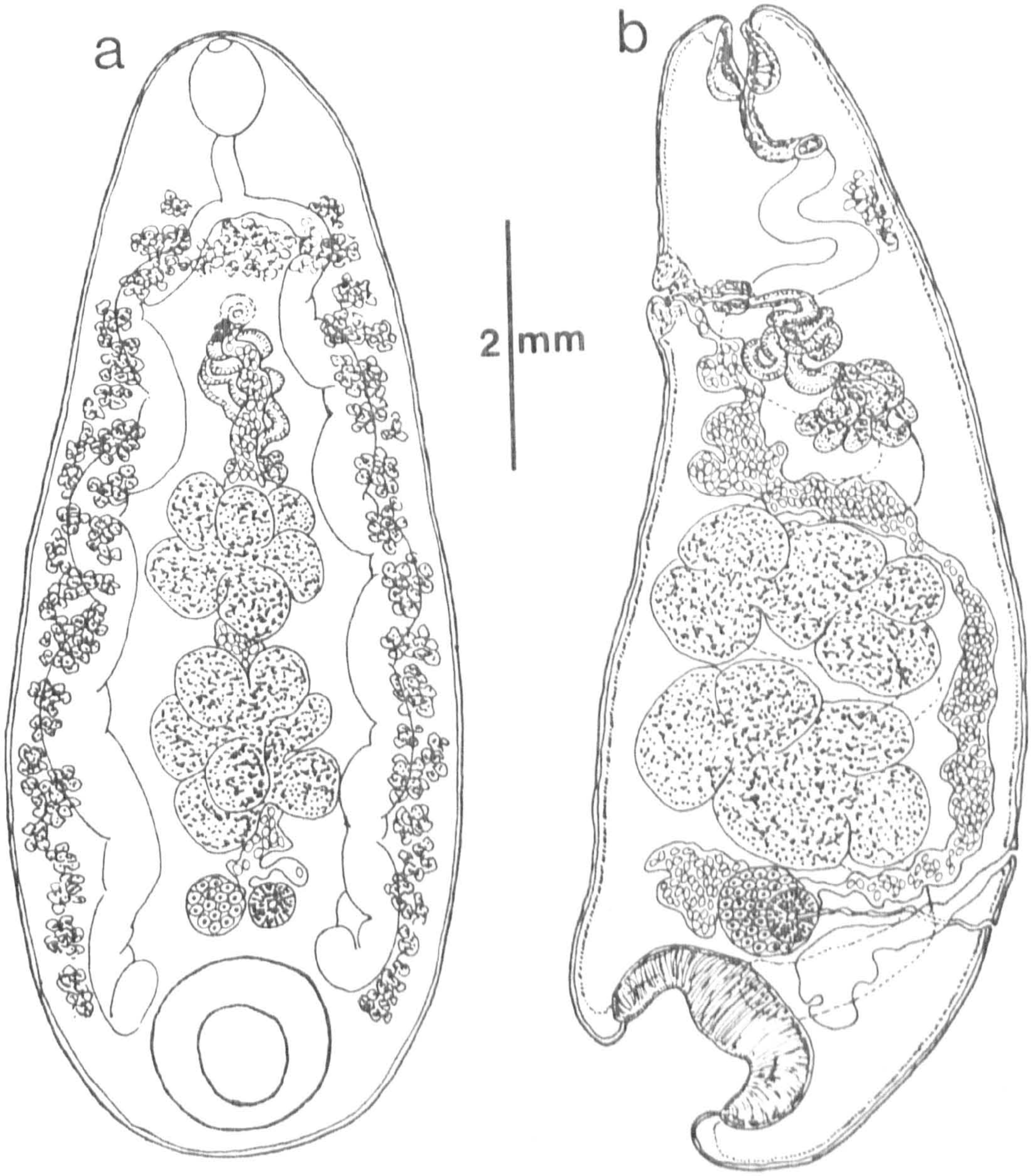

a
b
2 mm

FIGURE 93

Calicophoron sukari (Dinnik, 1954) n. comb.

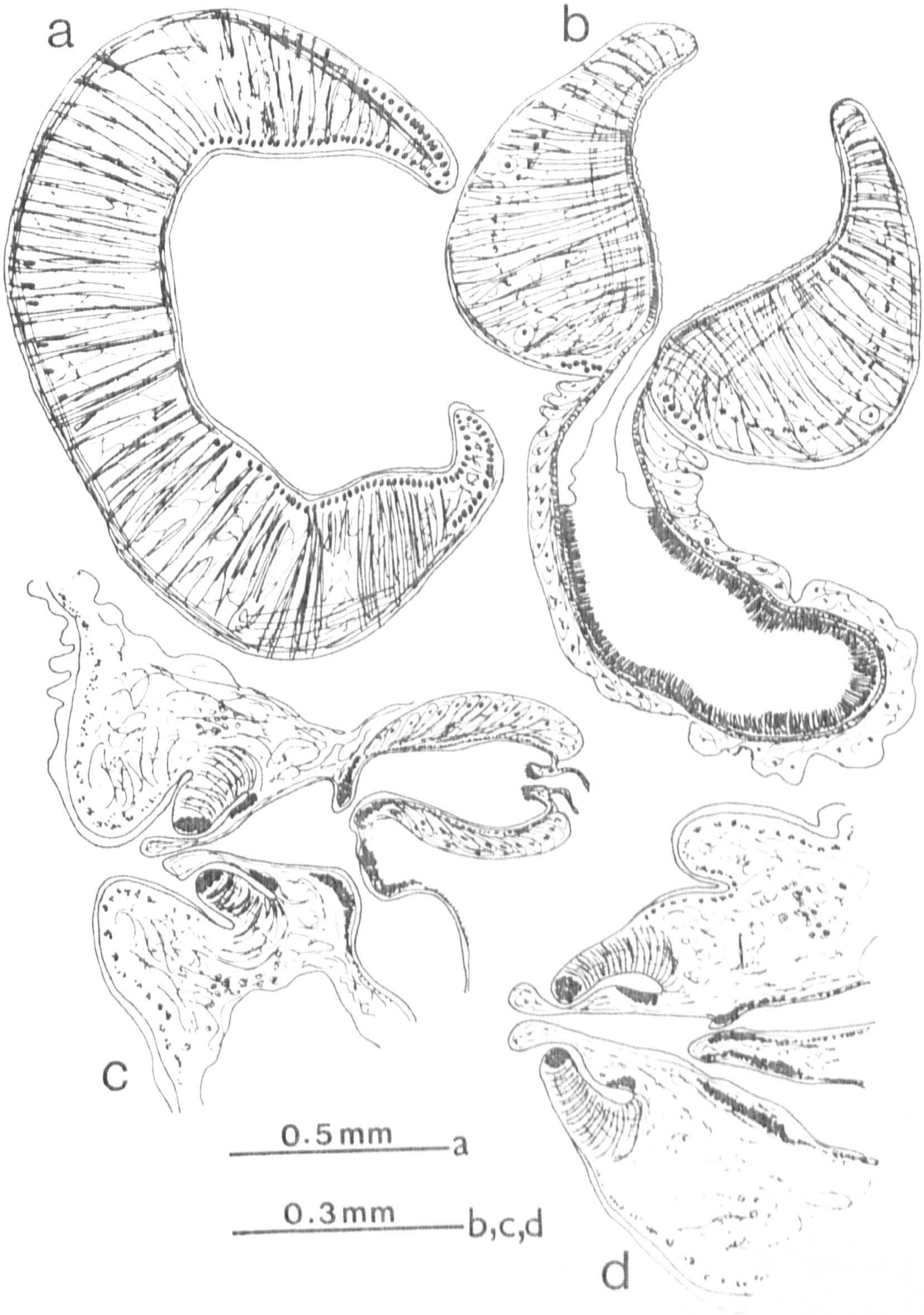
(median sagittal section)

a. Acetabulum (calicophoron type)

b. Pharynx (calicophoron type) and oesophagus. Note lumen of oesophagus with two kinds of lining, hyaline layer on anterior part and ciliated epithelium on posterior part.

c. Terminal genitalium (microbothrium type), retracted form and pars prostatica

d. Terminal genitalium (microbothrium type), relaxed form


a
b
C
0.5mm
a
0.3mm
b,c,d
d

Calicophoron phillerouxi (Dinnik, 1961) n. comb.

Synonyms: Paramphistomum vangrembergeni Van Strydonck, 1970
Paramphistomum togolense Albaret, Bayssade-Dufour, Guilhon, Kulo and Picot, 1978

TYPE SPECIMENS: British Museum (Natural History) Helminth Collection Number 1961.8.17.13-67 from the rumen of cattle in Mazabuka, Zambia (formerly Northern Rhodesia).

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collection

Aepyceros melampus	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Bos indicus	Chari, Baguirmi, Chad	Dr. F. Bertin
	Musuma, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Cattle	Mauritius	London School of Hygiene & Tropical Medicine, labeled "Cotylophoron cotylophorum".
	Freetown, Kabala, Sierra Leone	Commonwealth Institute of Helminthology coll. no. 336.
	Komatipoort, Transvaal, Republic of South Africa	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
	Chinsali, Mazabuka, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L LeRoux collection.

Damaliscus korrigum	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Kobus defassa	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Kobus defassa harnieri	Zaire	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Kobus kob	Uganda	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Kobus varondi	Mazabuka, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Redunca redunca	Mazabuka, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Syncerus caffer	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Namwala, Mazabuka, Zambia	London School of Hygiene & Tropical Medicine, Dr. P. L. LeRoux collection.
	Queen Elizabeth Park, Uganda	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Parc National Albert & Parc National Garamba, Zaire	Commonwealth Institute of Helminthology, Dr. J. A. Dinnik collection.

HABITAT: Rumen

DESCRIPTION:

Body conical, 5.10-10.36 mm long, 1.70-3.82 mm in the dorso-ventral direction. Body surface has papillae present around oral opening.

Acetabulum subterminal, external diameter 1.30-2.50 mm in the dorso-ventral direction; ratio to body length 1:3.2 to 1:4.0; of the paramphistomum type (sensu Näsmark, 1937) in median sagittal section; d.e.c.1 units sometimes compressed together to form a sphincter; number of circular muscle units, d.e.c.1, 14-24; d.e.c.2, 17-30; d.i.c., 38-53; v.e.c., 11-25; v.i.c., 40-56; m.e.c., 9-13.

Pharynx 0.70-1.01 mm long; 0.78-1.11 mm in the dorso-ventral direction; ratio to body length 1:7.1 to 1:10, to the diameter of the acetabulum 1:1.3 to 1:2.8; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section with weakly developed middle circular muscle units; internal surface has small dome-shaped papillae. Oesophagus 0.55-0.81 mm long; musculature of wall moderate and uniform in thickness, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form dorso-ventral bends, reach level of acetabulum with the blind ends directed dorsally.

Testes deeply lobed, directly tandem in posterior two third of the body; anterior testis 0.60-1.31 mm long, 0.80-2.98 mm in the dorso-ventral direction; posterior testis 1.10-1.24 mm long, 2.23-2.98 mm in the dorso-ventral direction; seminal vesicle deeply coiled and thin-walled; pars musculosa well developed, thick-walled and convoluted; pars prostatica well developed, 0.15-0.28 mm long and 0.15-0.16 mm wide.

Ovary round to subspherical, 0.59-0.68 by 0.78-0.91 mm, posttesticular and antero-dorsal to acetabulum; Mehlis' gland close to ovary, 0.39-0.45 by 0.55-0.57 mm; Laurer's canal crosses excretory vesicle or duct and opens on the dorsal surface about 0.40-1.80 mm posteriorly to the excretory pore; uterus winds forward dorsal to testes and ventral to the male ducts; vitellaria in lateral fields, extend from level of pharynx to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 130-157 by 67-85 µm.

Genital pore opens on the ventral surface at level of the oesophageal bifurcation or posterior to it, encircled by a round or oval swelling; terminal genitalium of the microbothrium type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level of the posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 94

Calicophoron phillerouxi (Dinnik, 1961) n. comb.

(SEM)

a. Whole worm, ventral view (scale bar = 400 µm)

b. Anterior end, note presence of large papillae around oral opening (scale bar = 100 µm)

c. Genital pore region, note oval swelling (scale bar = 100 µm)

d. Acetabular region (scale bar = 200 µm)

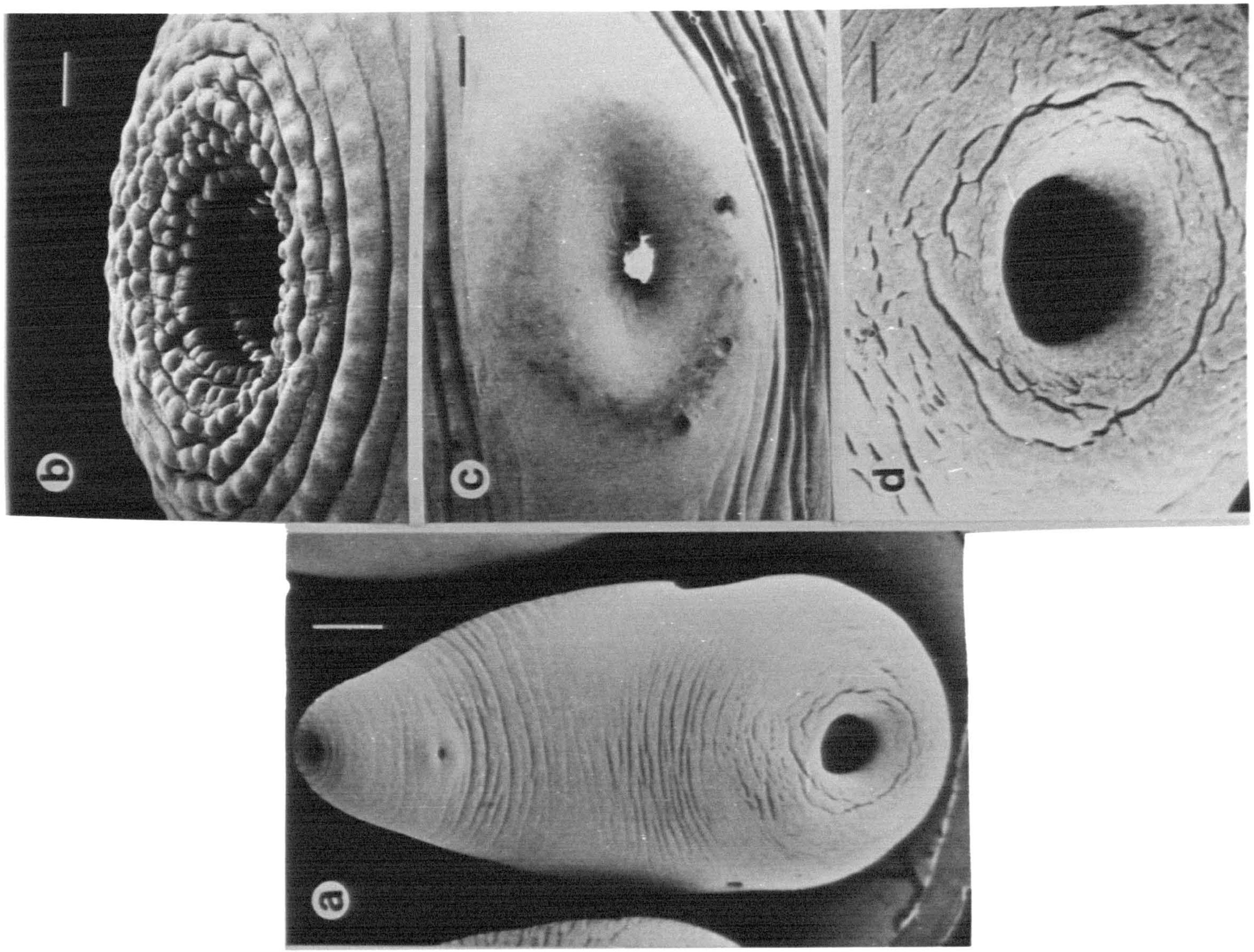

a
c
d
e

FIGURE 95

Calicophoron phillerouxi (Dinnik, 1961) n. comb.

a. Whole worm, ventral view

b. Whole worm, sagittal view

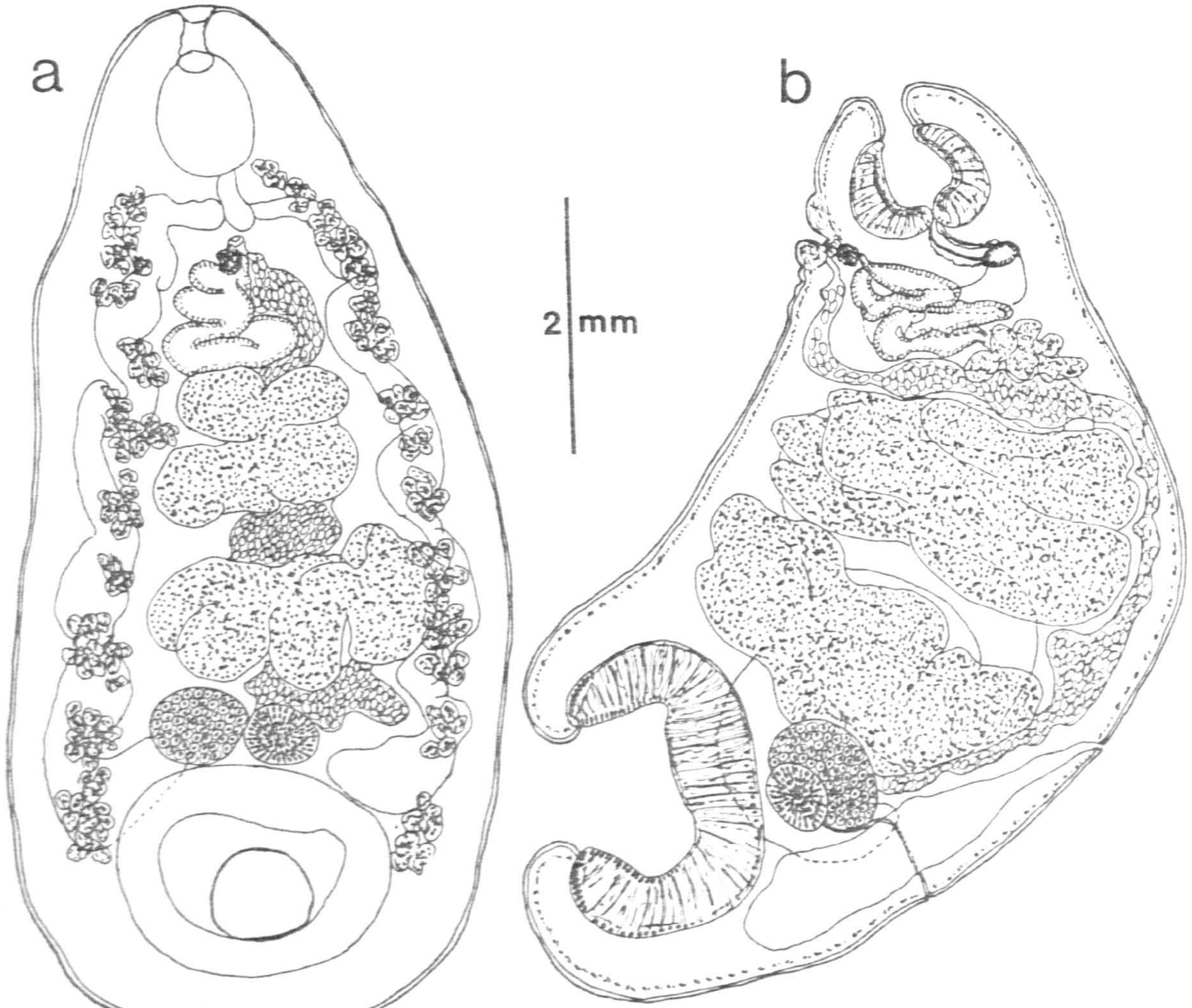

a
2 mm
b

FIGURE 96

Calicophoron phillerouxi (Dinnik, 1961) n. comb.

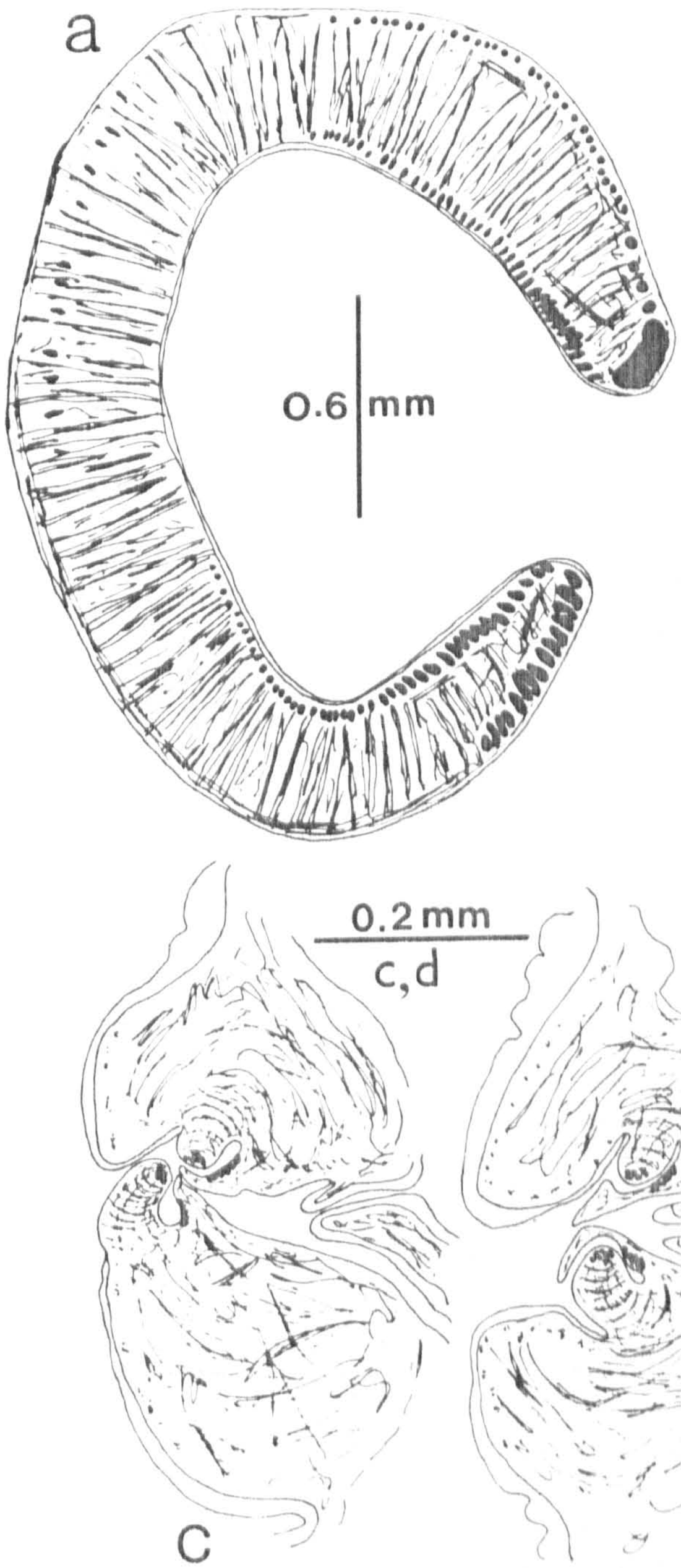
(median sagittal section)

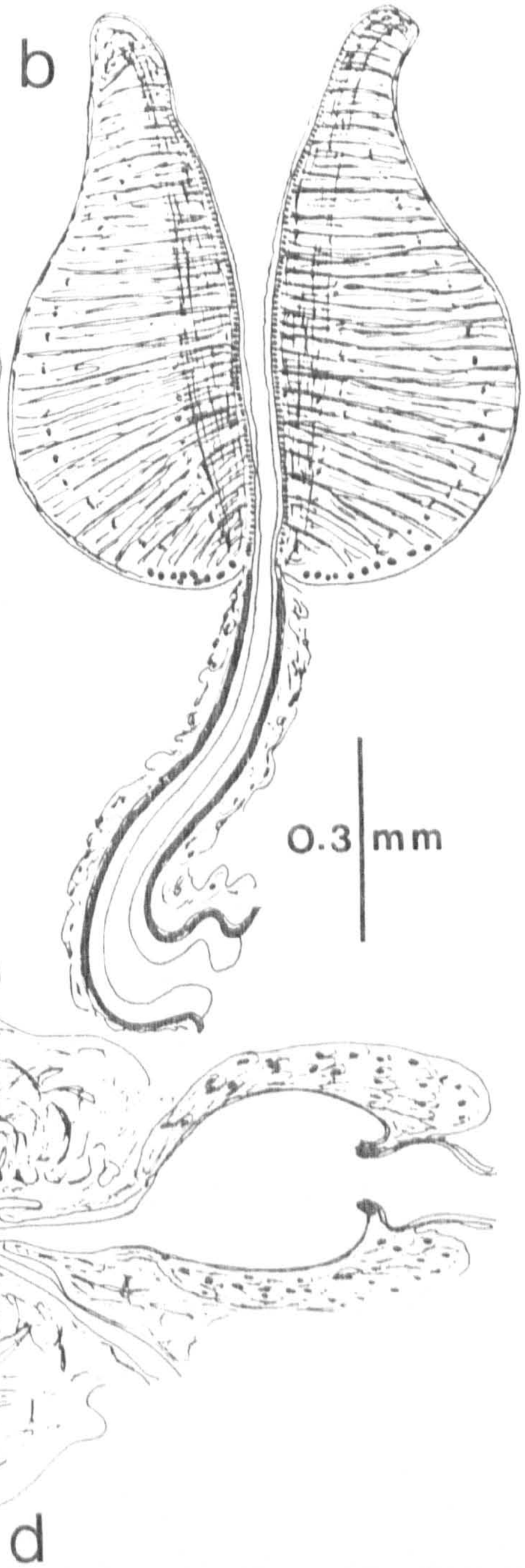
a. Acetabulum (paramphistomum type) with the d.e.c.l units developed into a sphincter

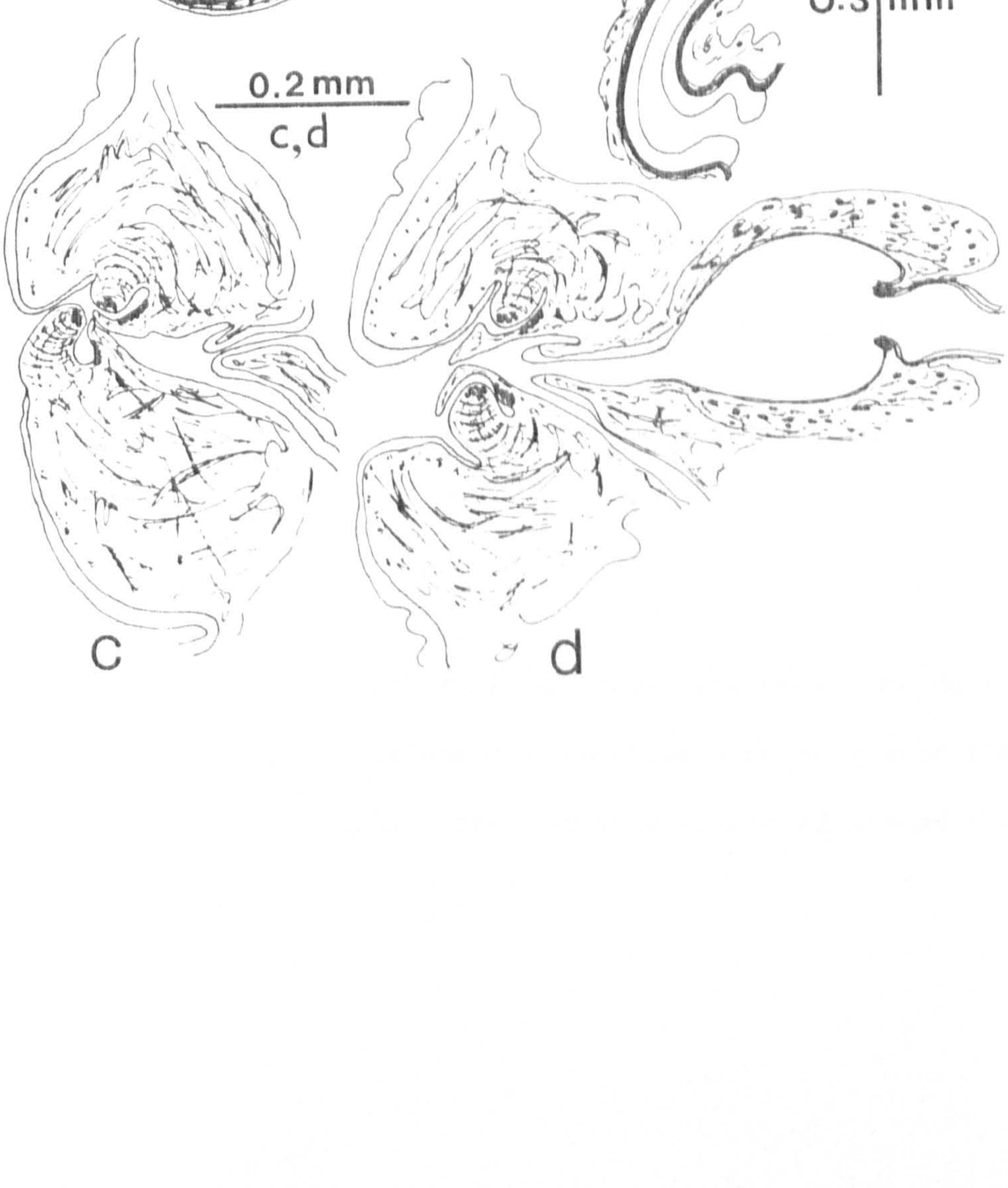
b. Pharynx (calicophoron type) and oesophagus

c. Terminal genitalium (microbothrium type),slightly retracted form

d. Terminal genitalium (microbothrium type), retracted form and pars prostatica


a
0.6 mm


b
0.3 mm


0.2 mm
c,d
c
d

Calicophoron daubneyi (Dinnik, 1962) n. comb.

TYPE SPECIMENS: British Museum (Natural History) Helminth Collection Number 1961.8.16.2-49, form the rumen of Bos taurus in Muguga, Kenya.

Commonwealth Institute of Helminthology, in Dr. J.A. Dinnik collection from the rumen of Bos taurus in Marula Estate, Naivasha, Kenya.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos indicus	Somalia	Commonwealth Institute of Helminthology coll. no. 57/80.
Bos taurus	Greece	Prof. Dr. C.A. Himonas
	Aquila and Rome Abattoirs, Italy	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
	Kenya	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Bolu, Turkey	Prof. Dr. Nevzat Güralp
Bubalus bubalis	Mengen, Turkey	Prof. Dr. Nevzat Güralp
Sheep	Aquila Abattoir, Italy	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.

HABITAT: Rumen

DESCRIPTION:

Body conical, 3.50-10.21 mm long, 2.34-4.11 mm in the dorso-ventral direction. Body surface has papillae present around the oral opening and much smaller ones sparsely scattered around the acetabular opening.

Acetabulum subterminal, 1.80-2.70 mm in external diameter in the dorso-ventral direction; ratio to body length 1:1.9 to 1:4.3; of the paramphistomum type (sensu Näsmark, 1937) in median sagittal section; d.e.c.1 units sometimes are compressed together to form a sphincter; number of circular muscle units, d.e.c.1, 14-20; d.e.c.2, 20-28; d.i.c., 39-56; v.e.c., 13-18; v.i.c., 39-48; m.e.c., 8-16.

Pharynx pear-shaped, 0.75-1.17 mm long, 0.85-0.96 mm in the dorso-ventral direction; ratio to body length 1:5.6 to 1:10.5, to the diameter of the acetabulum 1:2 to 1:2.5; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section with few and weakly developed middle circular units; internal surface has very small dome-shaped papillae. Oesophagus 0.39-0.62 mm long, musculature of wall moderate and uniform in thickness, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form dorso-ventral bends, reach level of acetabulum with the blind ends directed ventrally.

Testes deeply lobed, directly or slightly obliquely tandem in posterior two third of the body; anterior testis 1.30-1.53 mm long, 2.30-2.88 mm in the dorso-ventral direction; posterior testis 0,90-1.05 mm long, 2.42-2.83 mm in the dorso-ventral direction; seminal vesicle thin-walled and coiled; pars musculosa well developed, thick-walled and convoluted; pars prostatica well developed, 0.22-0.31 mm long and 0.31-0.33 mm wide.

Ovary round to subspherical, 0.50-0.58 by 0.54-0.82 mm, posttesticular and antero-dorsal to acetabulum; Mehlis' gland close to ovary, 0.39-0.66 by 0.38-0.66 mm; uterus winds forward dorsal to testes then ventral to the male ducts; Laurer's canal crosses excretory vesicle or duct and opens on the dorsal surface about 0.12-0.97 mm posteriorly to the excretory pore; vitellaria in lateral fields of the body, extend from level of pharynx to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 126-139 by 60-74 µm.

Genital pore opens on the ventral surface at level posterior to the oesophageal bifurcation; terminal genitalium of the microbothrium type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level of posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 97

Calicophoron daubneyi (Dinnik, 1962) n. comb.

(SEM)

a. Whole worm, ventral view (scale bar = 500 µm)

b. Genital pore region (scale bar = 100 µm)

c. Anterior end, note presence of large papillae (scale bar = 100 µm)

d. Another anterior end showing arrangement of papillae around oral opening (scale bar = 100 µm)

e. Acetabular region (scale bar = 200 µm)

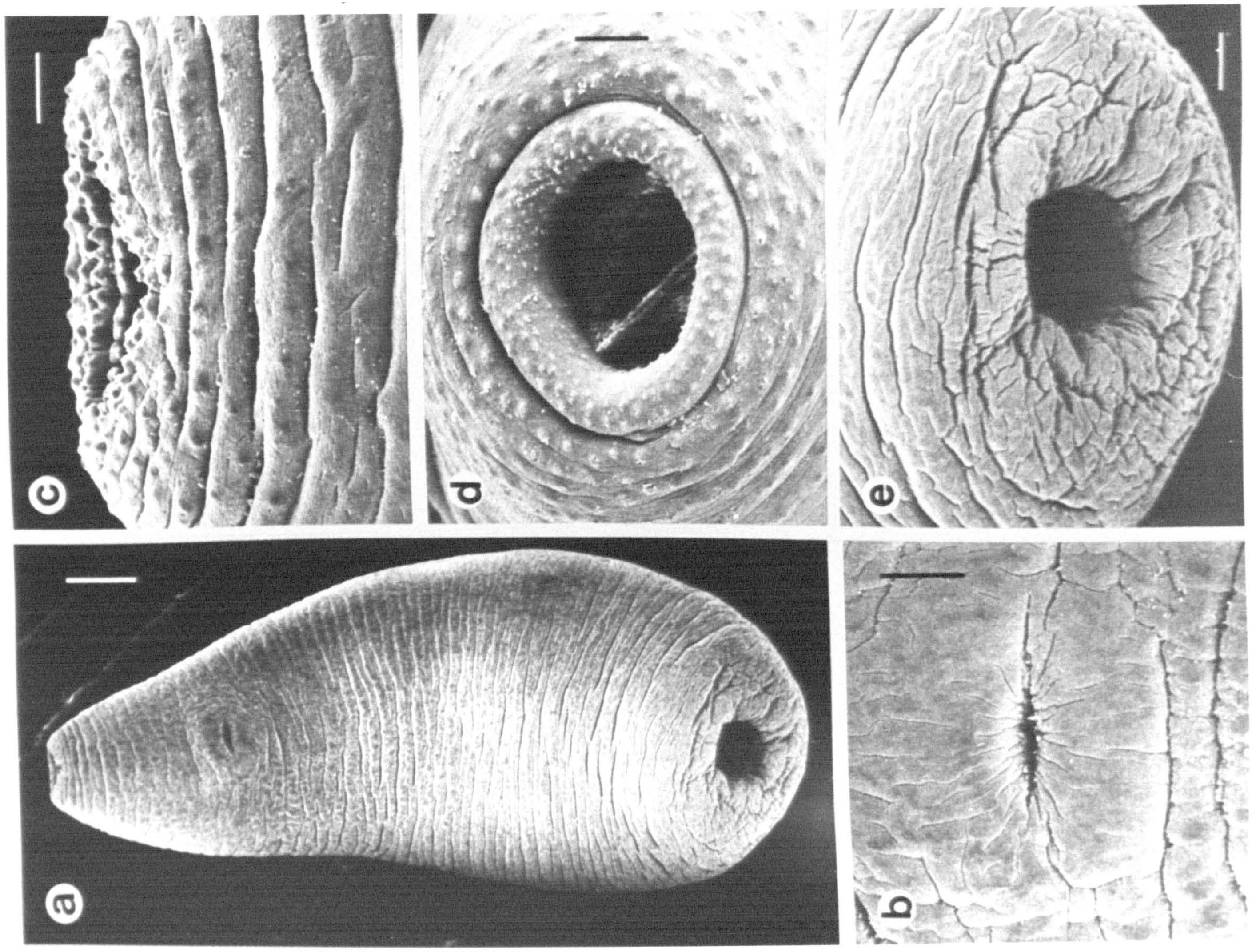

a
b
c
d
e

FIGURE 98

Calicophoron daubneyi (Dinnik, 1962) n. comb.

a. Whole worm, ventral view

b. Whole worm, sagittal view

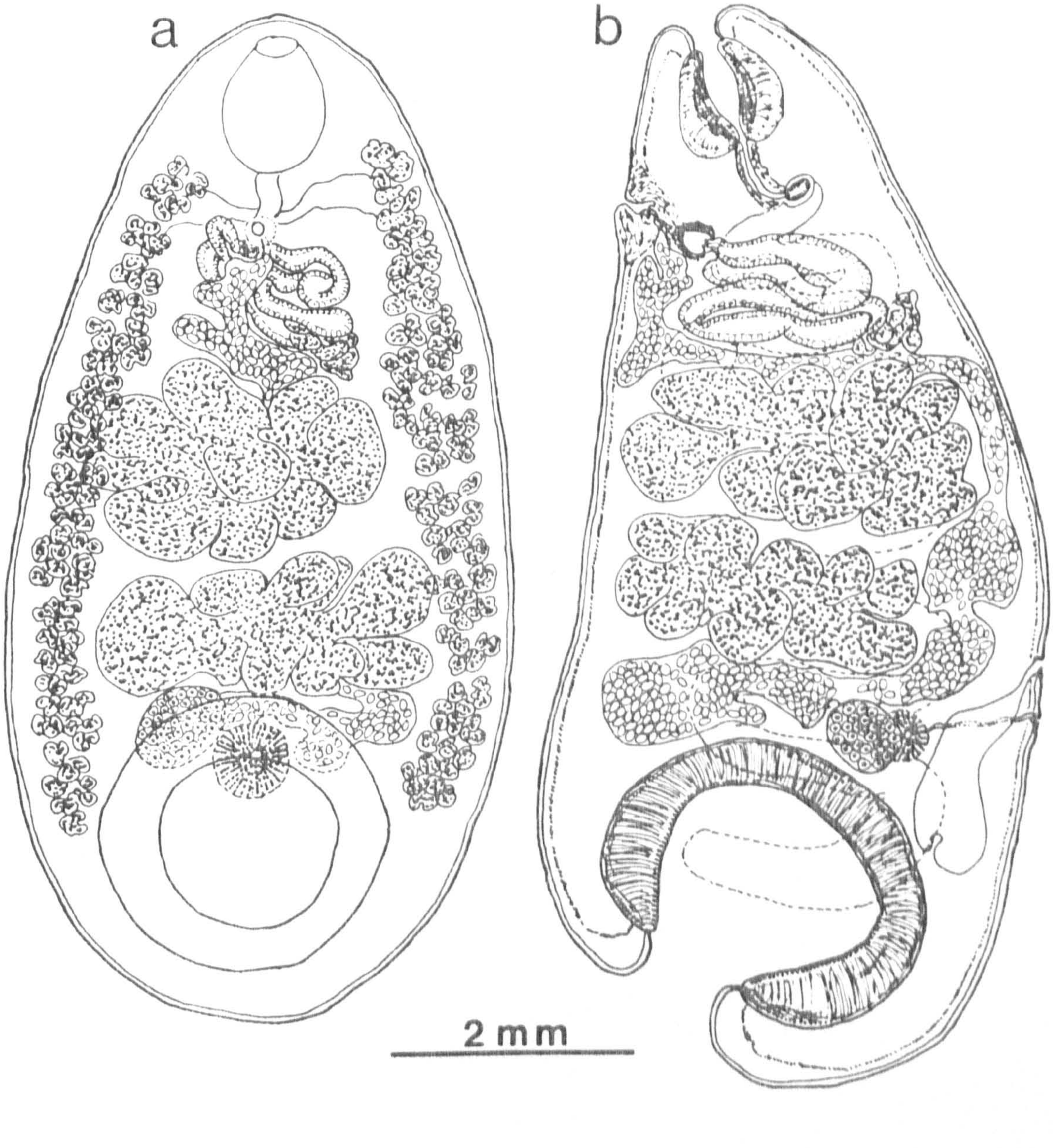

a
b
2 mm

FIGURE 99

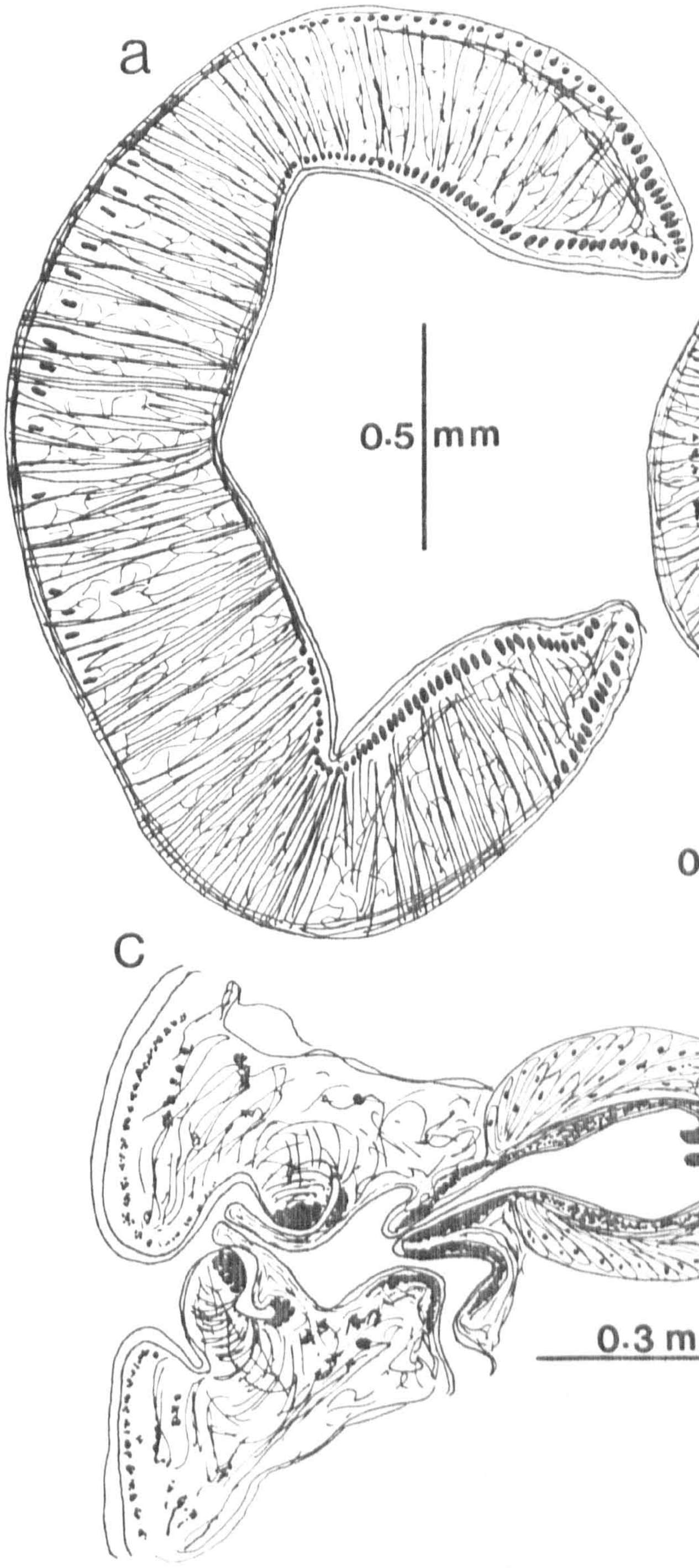
Calicophoron daubneyi (Dinnik, 1962) n. comb.

(median sagittal section)

a. Acetabulum (paramphistomum type)

b. Pharynx (calicophoron type) and oesophagus

c. Terminal genitalium (microbothrium type) and pars prostatica


a
0·5 mm
b
0·3 mm
C
0.3 mm

Calicophoron sukumum (Dinnik, 1964) n. comb.

TYPE SPECIMENS: British Museum (Natural History) Helminth Collection Number 1962.12.1-12, from the rumen of Bos indicus in Tanzania.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos indicus	Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Bos taurus	Cuba	Dr. J. Prokopič
	Mazabuka, Zambia	London Schoo of Hygiene & Tropical Medicine, Dr. P.L LeRoux collection.
Connochaetes taurinus	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection
Damaliscus korrigum	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Kobus defassa	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Kobus leche	Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Syncerus caffer	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J. A. Dinnik collection.
	Fort Jameson, Luangya Valley, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection
Taurotragus oryx	Serengeti, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.

HABITAT: Rumen

DESCRIPTION:

Body conical 7.82-9.86 mm long, 2.70-3.95 mm in the dorso-ventral direction. Body surface has few papillae around the oral opening and ventrally from this point to about the middle of the body. A round elevated area surrounding the genital pore is devoid of papillae.

Acetabulum subterminal; external diameter 1.69-2.62 mm in the dorso-ventral direction; ratio to body length 1:8.2 to 1:10.3, to the diameter of the acetabulum 1:1.5 to 1:3.1; of the pisum type (sensu Näsmark, 1937) in median sagittal section with the d.e.c.2 units irregularly spaced; number of circular muscule units, d.e.c.1, 18-25; d.e.c.2, 3-10; d.i.c., 39-57; v.e.c., 17-24; v.i.c., 45-68; m.e.c., 18-26.

Pharynx 0.86-1.00 mm long, 0.65-0.75 mm in the dorso-ventral direction; ratio to body length 1:8.2 to 1:10.3, to the diameter of the acetabulum 1:1.5 to 1:2.4; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section with few middle circular units; internal surface lined by very small dome-shaped papillae. Oesophagus 0.61-0.68 mm long, almost straight or may bend dorsally, musculature of wall moderate and uniform in thickness, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral fields, form more or less seven identical dorso-ventral bends, reach level of acetabulum with the blind ends directed ventrally.

Testes deeply lobed, directly or obliquely tandem in posterior two third of the body; anterior testis 1.16-1.56 mm long, 1.30-2.44 mm in the dorso-ventral direction; posterior testis

1.17-3.30 mm long, 2.04-2.81 mm in the dorso-ventral direction; seminal vesicle thin-walled and coiled; pars musculosa well developed, thick-walled and convoluted; pars prostatica well developed, slightly greater in length than it is wide (0.33-0.52 mm long)

Ovary round to subspherical, posttesticular and preacetabular, 0.57-0.82 by 0.65-1.06 mm; Mehlis' gland close to ovary either on its right or left side, 0.40-0.45 by 0.40-0.62 mm; Laurer's canal crosses excretory vesicle or duct and opens on the dorsal surface about 0.20-0.87 mm posteriorly to the excretory pore; uterus winds forward dorsal to testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of pharynx to acetabulum, not confluent dorso-medially in their anterior and posterior limits; egg 140-163 by 69-82 µm.

Genital pore opens of the ventral surface at a level posterior to the oesophageal bifurcation, surrounded by a circular swelling devoid of papillae. Terminal genitalium of the microbothrium type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level of the posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 100

Calicophoron sukumum (Dinnik, 1964) n. comb.

(SEM)

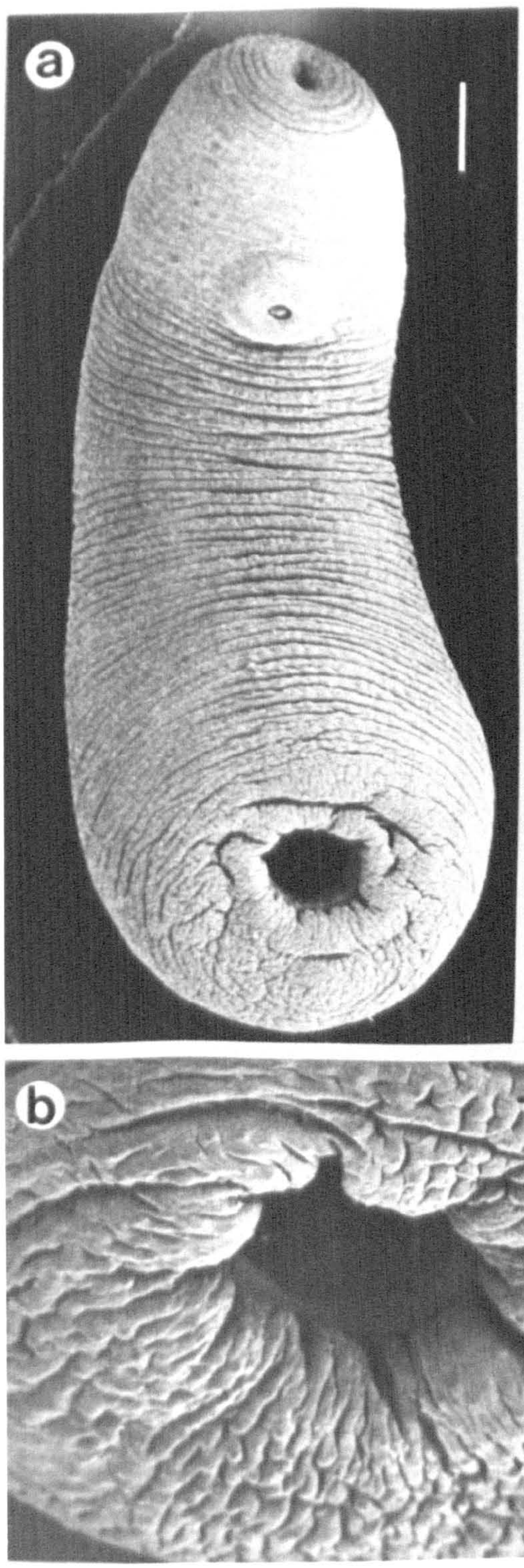
a. Whole worm, ventral view (scale bar = 500 µm)

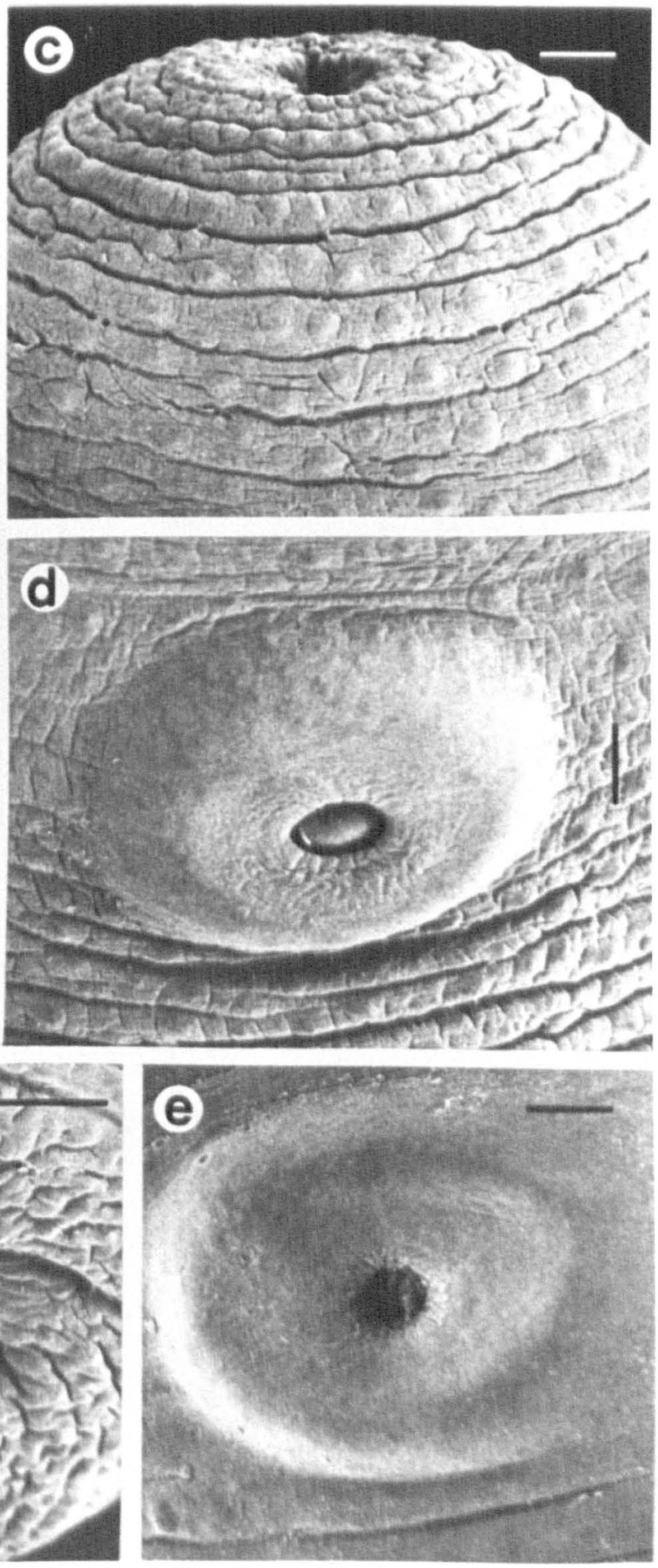
b. Acetabular region (scale bar = 200 µm)

c. Anterior end, note presence of dome-shaped papillae (scale bar = 100 µm)

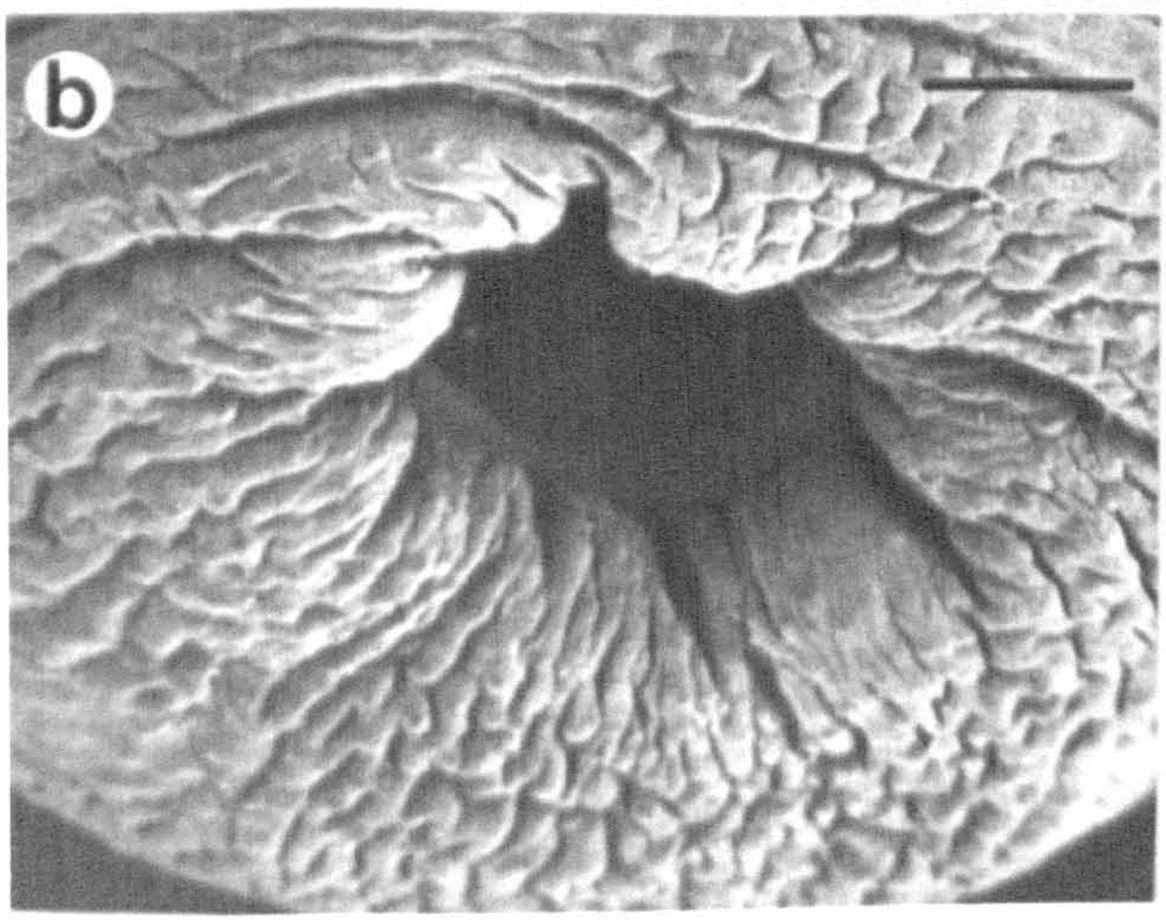
d. Genital pore region, note round swelling (scale bar = 100 µm)

e. Front view of another genital pore region, note the same circular swelling (scale bar = 100 µm)


a


c

d


b

e

FIGURE 101

Calicophoron sukumum (Dinnik, 1964) n. comb.

a. Whole worm, ventral view

b. Whole worm, sagittal view

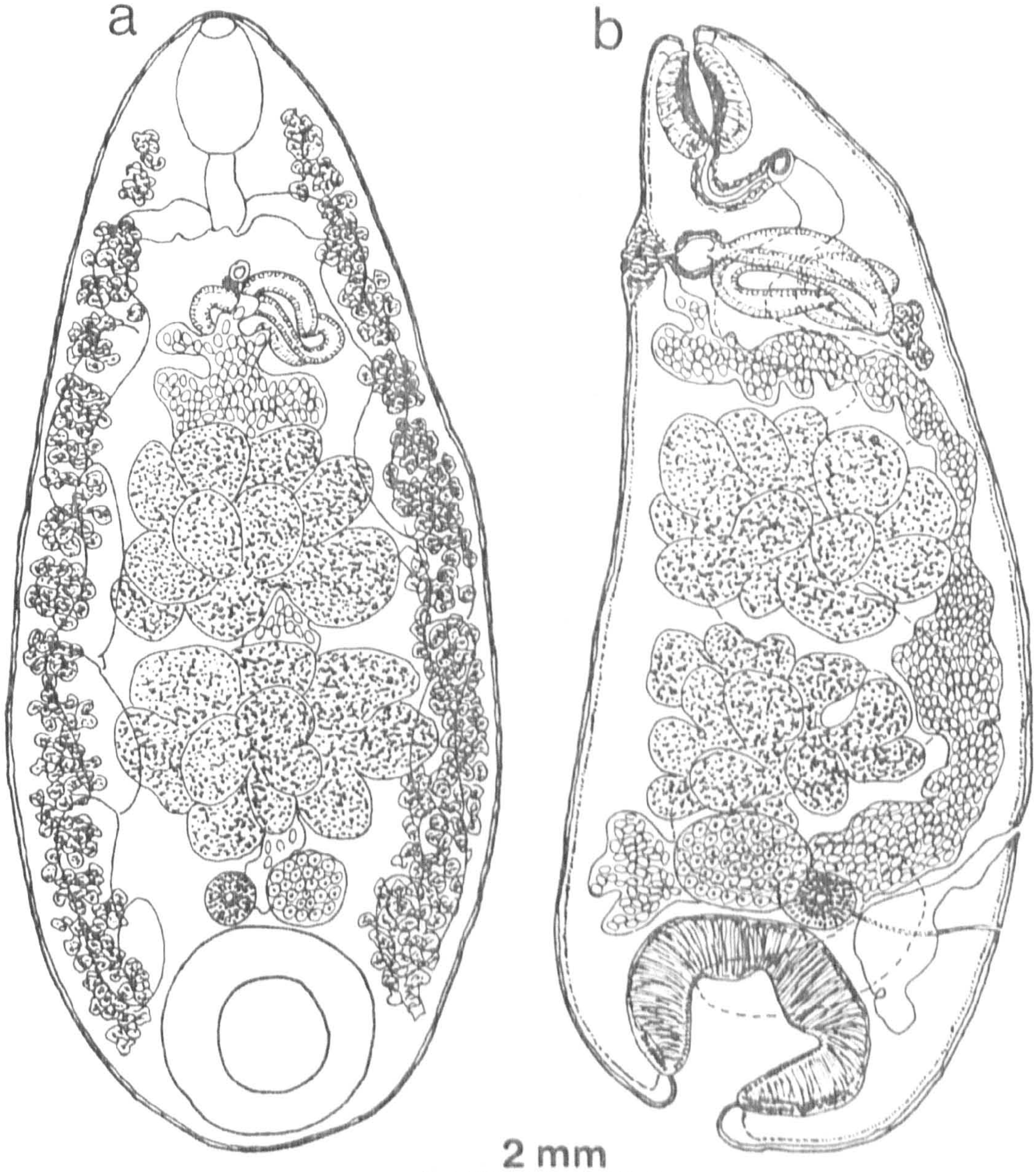

a
b
2 mm

FIGURE 102

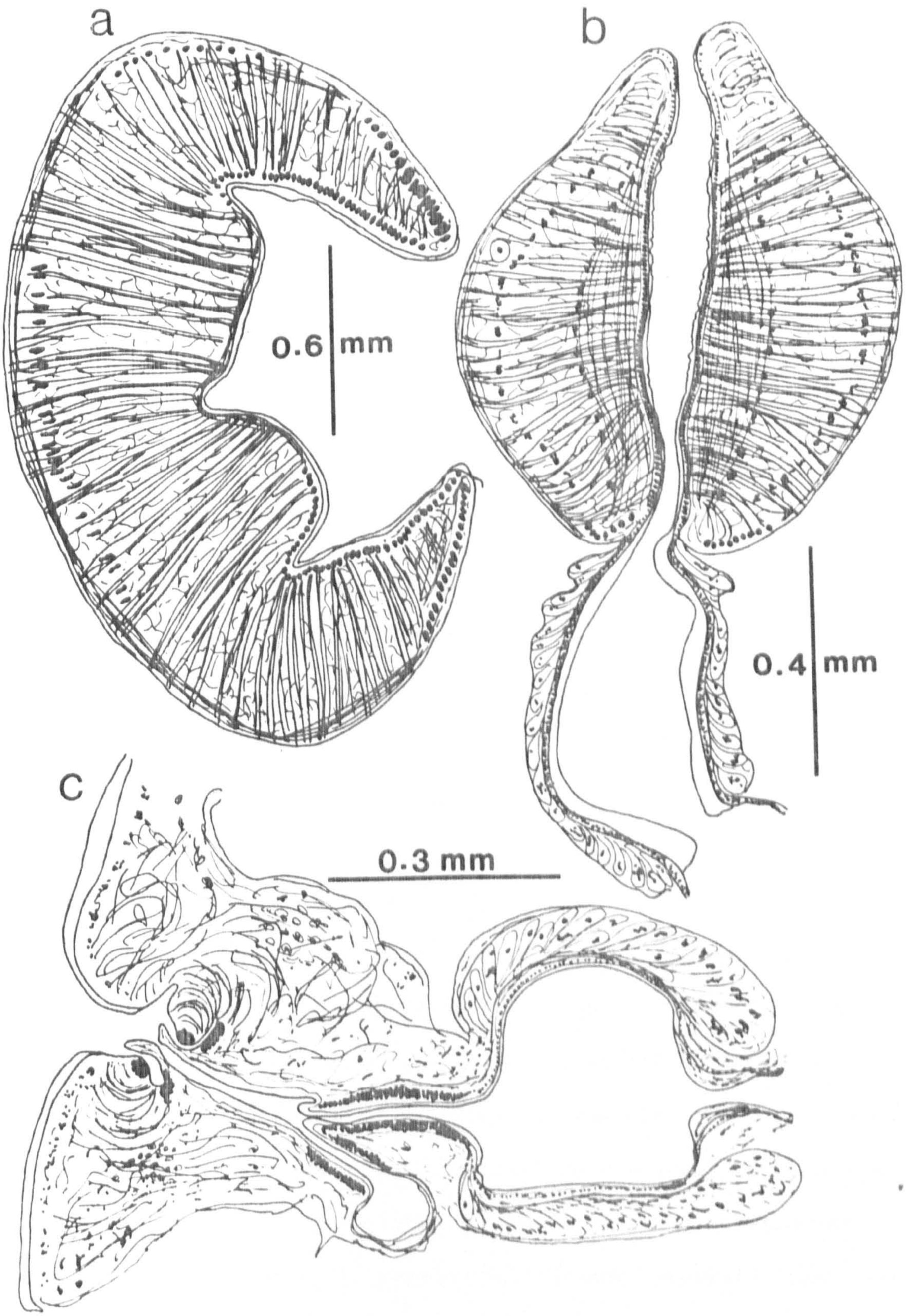
Calicophoron sukumum (Dinnik, 1964) n. comb.

(median sagittal section)

a. Acetabulum (pisum type)

b. Pharynx (calicophoron type) and oesophagus

c. Terminal genitalium (microbothrium type) and pars prostatica


a
0.6 mm
b
0.4 mm
C
0.3 mm

DISCUSSION

Calicophoron calicophorum, the type species of the genus was described originally by Fischoeder (1901, 1903) in the genus Paramphistomum under group "C" together with P. microbothrium, P. cotylophorum and P. bothriophoron because they are characterized by a well developed pars musculosa that separates them from the type and the rest of the species in the genus. Stiles and Goldberger (1910) removed P. calicophorum on the basis of the presence of a genital sucker and erected the genus Cotylophoron to contain it. Näsmark (1937) erected the genus Calicophoron for P. calicophorum and other species and gave the following as characters of the genus: i. general appearance intermediate between Paramphistomum and Gigantocotyle, ii. acetabulum of the calicophoron type, iii. terminal genitalium of the calicophoron type and iv. strongly developed pars prostatica. P. microbothrium and P. bothriophoron which were regarded by Fischoeder (1903) as closely related to P. calicophorum were retained in the genus Paramphistomum.

It was observed in the present study that it is very difficult to distinguish species of the genus Paramphistomum and Calicophoron by general appearance as given by Näsmark but species of the genus Gigantocotyle are easily separated from both genera because of the gigantic acetabulum. It was also observed that not all of the species assigned by Näsmark to the genus Calicophoron have the same type of acetabulum. The writer has re-examined Näsmark's material of C. raja as well as new materials from various hosts and localities in Africa and the species consistently showed an acetabulum type which is not of the type described by Näsmark

but of the pisum type because of the presence of a second group of circular units in the dorsal exterior series which are fewer and irregularly spaced. Not all of the species assigned by Näsmark to the genus also have the same type of terminal genitalium. Re-examination of the types of Paramphistomum papillosum Stiles and Goldberger, 1910 (loaned from the U.S. National Parasite Collection, USNMH Coll. No. 15025), a species assigned by Näsmark to the genus as well as additional materials from India and Indonesia revealed that the terminal genitalium of the species is of the papillogenitalis type (sensu Eduardo, 1980a) and not of the calicophoron type as claimed by Näsmark. Since he had no materials of this species or P. crassum and P. cauliorchis for examination, he only assumed that their acetabula and terminal genitalia are of the same type as that of C. calicophorum. Details of these structures were not given in the original descriptions of these species. Näsmark (1937) however failed to recognised the importance of the well developed pars musculosa which is obviously common to all species he assigned to the genus. Because of this failure, he retained some species ih the genus Paramphistomum which have this kind of pars musculosa, although by this, they differ from the type and other species of that genus. Fischoeder himself must have realized the value of this character since he employed it in subdividing the genus Paramphistomum into groups.

In the present study, the genus Calicophoron Näsmark, 1937 is recognised but redefined. The species assigned by Näsmark are also retained in the genus. However, the species he retained under the genus Paramphistomum as well as species subsequently described under that genus which are characterized by a well

developed pars musculosa are moved to the genus Calicophoron in new combinations. These are: Calicophoron bothriophoron (Braun, 1892), C. microbothrium (Fischoeder, 1901), C. papilligerum (Stiles and Goldberger, 1910), C. skrjabini (Popova, 1937), C. clavula (Näsmark, 1937), C. microbothrioides (Price and McIntosh, 1944), C. sukari (Dinnik, 1954), C. phillerouxi (Dinnik, 1961), C. daubneyi (Dinnik, 1962), C. sukumum (Dinnik, 1964), C. vangrembergeni (Van Strydonck, 1970) and C. togolense (Albaret, Bayssade-Dufour, Guilhon, Kulo and Picot, 1978). However, as will be shown later, three of the above species are junior synonyms.

Calicophoron ijimai was described originally by Fukui (1922a) under the genus Paramphistomum as a new species but later (1929) he synonymized it and P. calicophorum with P. explanatum. Näsmark (1937) however maintained it as a valid species and assigned it to his genus, Calicophoron. Although the species closely resembles C. calicophorum, he argued that they differ in the size and structure of the pharynx. He gave the size of the pharynx of C. calicophorum to range from 1.5 to 2 mm (mean 2 mm) and for C. ijimai only a mean value of 0.95 mm (no range given) and also claimed that the structure of the pharynx in the two species differs, being the calicophoron and ijimai types respectively. From his definition of these types, the only apparent differences include the interior circular muscle units which are well developed and the presence of a posterior sphincter in the ijimai type but are less developed and absent respectively in the calicophoron type. Yamaguti (1939) examined two sets of serial sections of P. ijimai loaned to him by Fukui and came to the conclusion that the

species in question is identical in all respects with Calicophoron calicophorum. He maintained this synonymy in his later works (1958, 1971). Lee and Lowe (1971) also regarded both species synonymous but under the genus Paramphistomum. Although Skrjabin (1949) accepted the validity of C. ijimai, he examined no materials of the species.

The writer has re-examined Näsmark's materials of C. ijimai and C. calicophorum loaned from the Naturhistoriska riksmuseet in Stockholm. Those of the former species consisted of eight specimens sectioned sagittally and some appeared to be greatly contracted. In these specimens, their pharynges measured from 0.92 to 1.48 mm long. Those of the latter species consisted of only two specimens sectioned sagittally and their pharynges measured 0.9 and 1.53 mm long, thus overlapping those of C. ijimai. Durie (1951) in Australia and Lee and Lowe (1971) in Malaysia in their materials of the species gave pharynx measurements of 0.73-1.5 and 1.35-1.8 mm long respectively. The writer has also examined new materials of C. calicophorum from various hosts and localities in Asia and Australia and some specimens showed pharynx measurements as low as or even lower than the values given by Näsmark for C. ijimai. Re-examination of Näsmark's materials of C. ijimai also revealed that only two of the eight specimens showed the presence of a posterior sphincter-like structure but it is not as well developed as that illustrated by him for the species. In these two speciemns, their pharynges appeared strongly contracted which may account for the interior circular muscle units particularly those at the base of the pharynx to have come closer together giving a false impression of a sphincter and this was mistaken by Näsmark as the posterior sphincter. Dinnik (1964) after a

comparative study of the pharyngeal structure of several paramphistomid species from different localities has shown convincingly that none of the differences given by Näsmark (1937) to separate the calicophoron, ijimai and paramphistomum types of pharynges were found great enough to justify differentiation of the three into separate structural types. He therefore regarded all three as one type, the calicophoron type. This study confirms Dinnik's view that the three above types are one and the same type. It is clear from the above that the characters employed by Nasmark (1937) in separating C. ijimai from C. calicophorum are subject to variations. The synonymy of the two species is here confirmed, C. calicophorum has priority over C. ijimai.

Stiles and Goldberger (1910) described P. crassum and P. cauliorchis from Bos indicus in India as new species. Both appear to be young forms as no eggs were observed. Näsmark (1937) moved both species to his genus Calicophoron but examined no materials of them. Skrjabin (1949) accepted their validity without examining types or new materials. Yamaguti (1958, 1971) merely listed both as separate species under Calicophoron while Mukherjee and Chauhan (1965) regarded P. crassum as a synonym of C. calicophorum. Re-examination of the type specimens of P. crassum (USNMH Coll. No. 7156) and P. cauliorchis (USNMH Coll. No. 7155) loaned from the U.S. National Parasite Collection, Beltsville, Maryland revealed that both species are identical with C. calicophorum. Slight differences on the size and relative position of the testes may be attributed to the fact that both species were young specimens. Paramphistomum crassum Stiles and Goldberger, 1910 and P. cauliorchis Stiles and Goldberger, 1910 are therefore regarded here as synonyms of

Calicophoron calicophorum (Fischoeder, 1901) Näsmark, 1937.

Calicophoron erschovi was established by Davydova (1959) for specimens recovered from cattle in the Primorsk Region of the U.S.S.R. The species was separated from C. calicophorum only by the presence of "cuticular papillae" on the anterior end. In this study, all specimens of C. calicophorum examined from various hosts and localities also revealed consistently the presence of tegumental papilla on their anterior ends. In the helminth collection of the Commonwealth Institute of Helminthology is a whole mount of C. erschovi labeled "type" presented by the author to Dr. Sheila Willmott on the latter visit to Moscow. There are also several sagittal sections made by Dr. J.A. Dinnik from specimens determined by the same author (Davydova) as C. erschovi. Examination of these materials revealed without doubt that the species in question is identical with C. calicophorum and should be synonymized with it.

Calicophoron orientalis was described by Mukherjee (1966) from Capra hircus in Bareilly, India. The species is closely related to C. calicophorum but was separated from the latter only by slight differences in body size and organ measurements. The type specimens could not be traced but from the author's own description and illustration, the species is identical with C. calicophorum and should be synonymized with it. The smaller measurements of C. orientalis may be attributed to the fact that specimens were recovered from a goat. It has been shown experimentally by Horak (1967) and Dinnik and Dinnik (1954) that in C. microbothrium, specimens of the same age recovered from goats and sheep are much smaller than those from cattle.

Davydova (1961) described Ceylonocotyle petrovi from Cervus nippon in Russia. However, after a careful and more detailed examination of the original material and additional specimens, the same author under her married name (Velichko, 1966a) moved the species under the genus Paramphistomum in a new combination. The type specimens could not be obtained but from the author's original description and illustration (Davydova, 1961) and redescription (Velichko, 1966a), the species in question agrees in all details with Calicophoron microbothrioides and should be synonymized with it.

Paramphistomum vangrembergeni was described by Van Strydonck (1970) from bovidae and Kobus sp. in the Belgian Congo (now Zaire). P. togolense was described by Albaret, Bayssade-Dufour, Guilhon, Kulo and Picot (1978) from specimens recovered from sheep experimentally infected with metacercariae from cercariae emitted by naturally infected Bulinus (bulinus) forskalii collected near Lomé, Togo. Both species belong to the genus Calicophoron because of the well developed pars musculosa. However, re-examination of the type specimens of the former loaned from the Musée Royal de l'Afrique Centrale, Tervuren (34310 holotype, 5058/610/B paratype) and co-types of the latter presented by the author (Dr. Albaret) revealed that both species are identical with Calicophoron phillerouxi. Although P. togolense has the same intermediate host as C. phillerouxi, the authors argued that the sporocyst in the former is V-shaped while in the latter, it is not. The stability of this shape is very doubtful as it may be influenced by the surrounding tissue of the intermediate host envelopping it. Lengy (1960) has shown different shapes of the sporocyst of C. microbothrium at different ages, spherical (8-12 hours), oval (24 hours to 4 days),

sausage shape (8 days) with deep transverse constriction along its length which may bend to form a U- or V-shape. It is possible that Albaret et al have observed the latter stage. Paramphistomum vangrembergeni and P. togolense are therefore regarded here as synonyms of Calicophoron phillerouxi.

Most recently, Wang (1979) described Calicophoron zhejiangense and C. wuchengense as new species both from Bubalus bubalis in China. The former was described to be closely related to C. papillosum but differentiated from it by the caeca having more spirals and in having different ratios of the acetabulum and pharynx in relation to the body length. The latter was described to be closely related to C. calicophorum and C. cauliorchis but differentiated from both in having acetabulum and terminal genitalium of the calicophoron types, testes side by side or diagonal and in having different ratios of acetablum and pharynx in relation to the body length. The numbers of spirals or dorso-ventral bends of the caeca of C. zhejiangense given by Wang were 6 to 8 which are also the numbers observed in C. papillosum specimens examined in this study. Stiles and Goldberger (1910) in their illustration of the caeca of the latter species showed 8 dorso-ventral bends. The ratios of the acetabulum and pharynx in relation to the body length employed by Wang to differentiate his species from closely related ones are not stable characters. It has been shown by some workers (Horak, 1967 and Dinnik unpublished) and also observed in the present study that body length in paramphistomids varies greatly and is affected by various factors like the state of the worm during fixation, manner of fixation and the kind of fixative used. Consequently, any ratio of the body length in relation to other organs of the body also varies considerably.

Wang has also erred in claiming that C. wuchengense differs from C. calicophorum by having a calicophoron type of acetabulum and terminal genitalium because the latter species has been described and re-described by several workers (Näsmark, 1937; Durie, 1951; Lee and Lowe, 1971) and also observed in this study to possess the same type of acetabulum and terminal genitalium. The measurement values given by Wang to differentiate his species from closely related ones are too small not, allowing for variations. C. zhejiangense and C. wuchengense are therefore regarded here as junior synonyms of C. papillosum and C. calicophorum respectively.

Stiles and Goldberger (1910) established Bothriophoron as a subgenus under Paramphistomum for P. bothriophoron (Braun, 1892) and P. papilligerum Stiles and Goldberger, 1910 on account of the presence of a very large "ventral chamber" (= ventral atrium of Näsmark, 1937). Grétillat (1958) examined and identified specimens from zebu cattle in Madagascar (type locality of the species) as identical with that originally described as Amphistomum bothriophoron by Braun (1892). He supported Stiles and Goldberger's erection of Bothriophoron and proposed for its elevation to full generic rank. He distinguished Bothriophoron from Paramphistomum by the following characters: presence of an enormous genital atrium (= ventral chamber or ventral atrium), thick genital sphincter, presence of a non muscular pre-oesophageal organ and small size of miracidium. As shown in the description of the various species in this study, the structure of the terminal genitalium varies in different species in the same genus and therefore is only of specific and not of generic value. Grétillat himself (1964a) has shown that the structure of the terminal genitalium of the species in the genus Carmyerius Stiles

and Goldberger, 1910 of the family Gastrothylacidae (pouched amphistomes) where some species are characterized by a large ventral atrium, can only be utilized as a specific character. The size of the miracidium can hardly be justified as a generic character. The writer has also examined several specimens of P. bothriophoron from Madagascar and Kenya. What was regarded by Grétillat (1958) as a non-muscular pre-oesophageal organ is actually the anterior part of the oesophagus which has the normal lining of a hyaline layer. The rest is lined by ciliated epithelium similar to that found lining the caeca. These two kinds of oesophageal linings have also been observed in some species in other genera. Fukui (1929) first observed these in Fischoederius cobboldi and confimed in this work from specimens of this species from the Philippines, India and Malaysia. These were also observed in the present study in Gigantocotyle symmeri and Calicophoron sukari. It appears therefore that the type of oesophageal lining has no generic value but rather can only be employed as a specific character. It is clear that Bothriophoron's elevation to full generic rank by Grétillat (1958) or its establishment as a subgenus by Stiles and Goldberger (1910) was based on characters which are only of specific value. Bothriophoron bothriophoron belongs to the genus Calicophoron because of the well developed pars musculosa. Consequently, the genus Bothriophoron Grétillat, 1958 becomes a junior synonym of Calicophoron Näsmark, 1937.

As already explained under the genus Paramphistomum, the species Paramphistomum microon Railliet, 1924 which was moved by Näsmark (1937) to the genus Calicophoron in a new combination without examining materials of it, is regarded here as a species inquirenda.

Only the following species previously assigned by Näsmark (1937) to the genus Calicophoron are considered valid: Calicophoron calicophorum (Fischoeder, 1901) Näsmark, 1937; C. papillosum (Stiles and Goldberger, 1910) Näsmark, 1937 and C. raja Näsmark, 1937.

The following species previously described under the genus Paramphistomum are considered valid and moved to the genus Calicophoron in new combinations because of the well developed pars musculosa: Calicophoron microbothrium (Fischoeder, 1901), C. papilligerum (Stiles and Goldberger, 1910), C. clavula (Näsmark, 1937), C. microbothrioides (Price and McIntosh, 1944), C. sukari (Dinnik, 1954), C. phillerouxi (Dinnik, 1961), C. daubneyi (Dinnik, 1962) and C. sukumum (Dinnik, 1964).

The genus Bothriophoron (Stiles and Goldberger, 1910) Grétillat, 1958 is rejected and synonymized with Calicophoron. Consequently, the type and only species becomes Calicophoron bothriophoron (Braun, 1892) n. comb.

Calicophoron cauliorchis (Stiles and Goldberger, 1910) Näsmark, 1937; C. crassum (Stiles and Goldberger, 1910) Näsmark, 1937; C. ijimai (Fukui, 1922) Näsmark, 1937; C. erschovi Davydova, 1959; C. orientalis Mukherjee, 1966; C. wuchengense Wang, 1979 and Paramphistomum (Cauliorchis) skrjabini Popova, 1937 are all considered synonyms of Calicophoron calicophorum.

Calicophoron zhejiangense Wang, 1979 is regarded a synonym of Calicophoron papillosum. Paramphistomum vangrembergeni Van Strydonck, 1970 and P. togolense Albaret, Bayssade-Dufour, Guilhon, Kulo and Picot, 1978 are both considered synonyms of Calicophoron phillerouxi. Paramphistomum petrovi (Davydova, 1961) Velichko, 1966 is considered a synonym of Calicophoron microbothrioides.

To separate the valid species of the genus, a key is given below.

Key to the species of the genus Calicophoron Näsmark, 1937

1. True ventral atrium present - - - - - - - - - - - - - - - - - - - 2

   True ventral atrium absent - - - - - - - - - - - - - - - - - - - 3

2. Papillae present on wall of ventral atrium - - - C. papilligerum

   Papillae absent on wall of ventral atrium - - - C. bothriophoron

3. Terminal genitalium of the calicophoron type - - C. calicophorum

   Terminal genitalium of the raja type - - - - - - - - - - - C. raja

   Terminal genitalium of the clavula type - - - - - - - - C. clavula

   Terminal genitalium of the papillogenitalis type - C. papillosum

   Terminal genitalium of the microbothrium type - - - - - - - - 4

4. Oesophageal bulb present - - - - - - - - - - C. microbothrioides

   Oesophageal bulb absent - 5

5. Blind caecal ends directed dorsally - - - - - - - - - - - - - - 6

   Blind caecal ends directed ventrally - - - - - - - - - - - - - - 7

6. Caecal ends meet medially; bigger terminal
   genitalium - - - - - - - - - - - - - - - - - - C. microbothrium

   Caeca ends do not meet medially; smaller terminal
   genitalium - - - - - - - - - - - - - - - - - - C. phillerouxi

7. Posterior part of internal surface of oesophagus lined by
   ciliated epithelium; vitellaria confluent dorso-medially
   in their anterior limits - - - - - - - - - - - - - C. sukari

   Posterior part of internal surface of oesophagus not lined by
   ciliated epithelium; vitellaria not confluent
   dorso-medially - 8

8. Acetabulum of the paramphistomum type; circular elevated area around genital pore absent - - - - - - - - - - - - C. daubneyi

Acetabulum of the pisum type; circular elevated area around genital pore present - - - - - - - - - - - - C. sukumum

Revision of the genus Gigantocotyle Näsmark, 1937 and elevation of the subgenus Explanatum Fukui, 1929 to full generic status

INTRODUCTION

Fukui (1929) established Explanatum as a subgenus under the genus Paramphistomum Fischoeder, 1901 to contain P. explanatum (Creplin, 1847) and P. formosanum Fukui, 1929 on the basis of the obliquely arranged and lobed testes and absence of a genital sucker. The former species was designated as the type of the subgenus. Later, Näsmark (1937) erected the genus Gigantocotyle for those species previously described under the genus Paramphistomum with dominating acetabulum and included under it among others the two species assigned by Fukui under his subgenus Explanatum. In new combinations, Näsmark transfered the following species: Gigantocotyle gigantocotyle (Brandes in Otto, 1896); G. explanatum (Creplin, 1847), G. bathycotyle (Fischoeder, 1901), G. fraternum (Stiles and Goldberger, 1910), G. siamense (Stiles and Goldberger, 1910), G. formosanum (Fukui, 1929) and G. birmense (Railliet, 1924). By tautonomy, Gigantocotyle gigantocotyle is the type species of the genus. He described Gigantocotyle symmeri and G. duplicitestorum as new species from cattle and hippopotamus respectively. Yeh (1957) described G. lerouxi as a new species from the red lechwe in North Rhodesia (now Zambia).

Yamaguti (1958, 1971) rejected the genus Gigantocotyle and synonymized it with Paramphistomum Fischoeder, 1901. He recognised Explanatum Fukui, 1929 as a subgenus of Paramphistomum and assigned all species of the genus Gigantocotyle Näsmark, 1937 under this subgenus because of their large acetabula. Baer and Joyeux (1961)

and Lee and Lowe (1971) accepted Yamaguti's synonymy but they did not recognise the subgeneric division of the genus Paramphistomum. Most authors however recognised the genus Gigantocotyle since they reported or redescirbed already known species under the genus based on new materials (Willmott, 1950a; Singh, 1958; Dinnik, Walker, Barnett and Brocklesby, 1963; Dollfus, 1963; Graber, Fernagut and Oumatie, 1966; Gupta, 1966; Kadhim, Altaif and Hawa, 1969, 1970; Tenora, Kotrlá and Blazek, 1974; Sey and Graber, 1979b) or included the genus in a systematic classification of the group (Skrjabin, 1949; Mukherjee and Chauhan, 1965).

Gigantocotyle Näsmark, 1937

GENERIC DIAGNOSIS EMENDED

Paramphistomidae, Paramphistominae. Body large and conical; curved ventrally, almost round in cross section; ventral pouch absent. Acetabulum subterminal and enormous in size. Pharynx without pouch or diverticle; oesophagus with or without bulb or posterior sphincter; caeca reach acetabular region, almost straight or sinuous in their course. Testes lobed or indented, directly or obliquely tandem or juxtaposed or obliquely horizontal; seminal vesicle long, deeply coiled and thin-walled; pars musculosa well developed, thick-walled and convoluted; pars prostatica well developed. Ovary and Mehlis' gland posttesticular; Laurer's canal crosses the excretory vesicle or duct; vitellaria in lateral fields, may or may not be confluent dorso-medially in their anterior and posterior limits. Genital sucker absent. Parasitic in the stomach and intestines of Artiodactyla.

Type species: Gigantocotyle gigantocotyle (Brandes in Otto, 1896) Näsmark, 1937

Gigantocotyle gigantocotyle (Brandes in Otto, 1896) Näsmark, 1937

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collection

Hippopotamus amphibius	Sudan	British Museum (Natural History) coll. no. 1952. 8.43.50.
	Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
	Parc National de la Garamba, Zaire	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.

HABITAT: Stomach

DESCRIPTION:

Body pyriform, tapers anteriorly, much broader and rounded posteriorly, 6.96-10.38 mm long, 4.00-5.56 mm in the dorso-ventral direction, strongly curved ventrally. Body surface lacks tegumental papillae.

Acetabulum enormous, subterminal, 3.96-6.00 mm in external diameter in the dorso-ventral direction; ratio to body length 1:1.4 to 1:2.4; of the gigantocotyle type (new type) in median sagittal section characterized by the presence of a second group of circular muscle units in the dorsal and ventral exterior circular series; number of circular muscle units, d.e.c.1, 10-20; d.e.c.2, 36-53; d.i.c., 42-56; v.e.c.1, 15-18; v.e.c.2, 6-12; v.i.c., 46-55; m.e.c., 9-15.

Pharynx 1.15-1.53 mm long, 1.35-1.50 mm in the dorso-ventral direction; ratio to body length 1:4.5 to 1:7.8, to the diameter of

the acetabulum 1:2.5 to 1:3.3; of the explanatum type (sensu Näsmark, 1937) in median sagittal section; internal surface smooth, devoid of papillae. Oesophagus 1.28-1.62 mm long, musculature of wall moderate and uniform in thickness, no bulb or posterior sphincter; lumen lined by thick hyaline layer throughout its length. Caeca in lateral sides of the body, nearly straight in their course, reach level of acetabulum with the blind ends directed posteriorly.

Testes lobed, obliquely horizontal in middle third of body and separated from each other by the uterus; right testis 1.50-1.83 mm long, 1.20-2.09 mm in the dorso-ventral direction; left testis 1.90-2.03 mm long, 1.30-1.86 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa well developed, thick-walled and convoluted; pars prostatica well developed, 0.62-0.85 mm long and 0.46-0.53 mm wide.

Ovary subspherical, 0.56-0.72 by 0.57-0.59 mm, dorsal to acetabulum and posterior to testes; Mehlis' gland close to ovary, 0.36-0.37 by 0.30-0.33 mm; uterus winds forward dorsally and in between the testes then ventrally to the male ducts; vitellaria in lateral fields, confluent dorso-medially both in their anterior and posterior limits; Laurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface about 0.66-0.93 mm posteriorly to the excretory pore; egg 100-122 by 66-80 m.

Genital pore opens on the ventral surface at the tip of a well developed and thick genital papilla at about a level posterior to the oesophageal bifurcation; terminal genitalium of the gigantocotyle type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface anteriorly to the Laurer's canal opening.

FIGURE 103

Gigantocotyle gigantocotyle (Brandes in Otto, 1896)
Näsmark, 1937
(SEM)

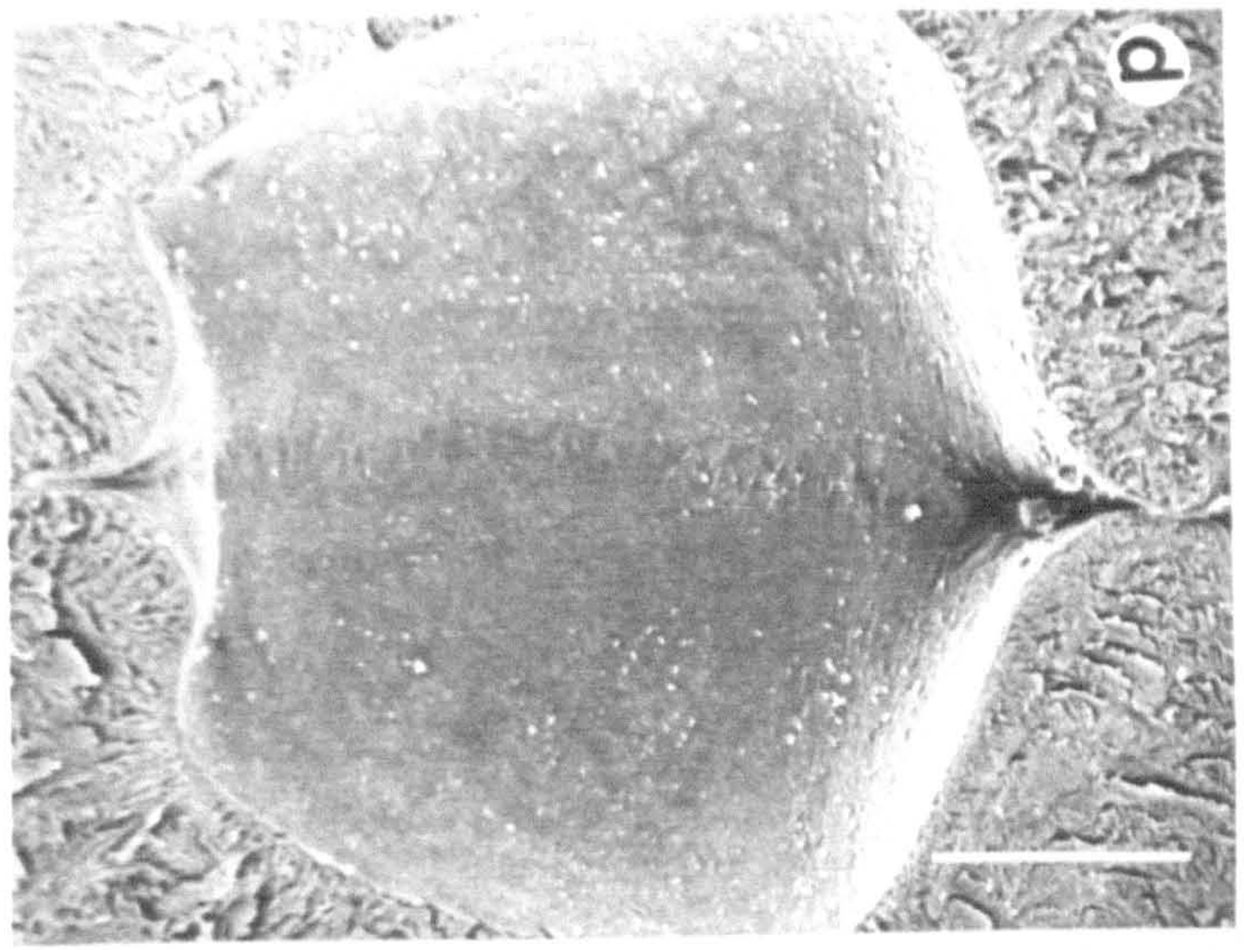
a. Whole worm, ventral view (scale bar = 1 mm)

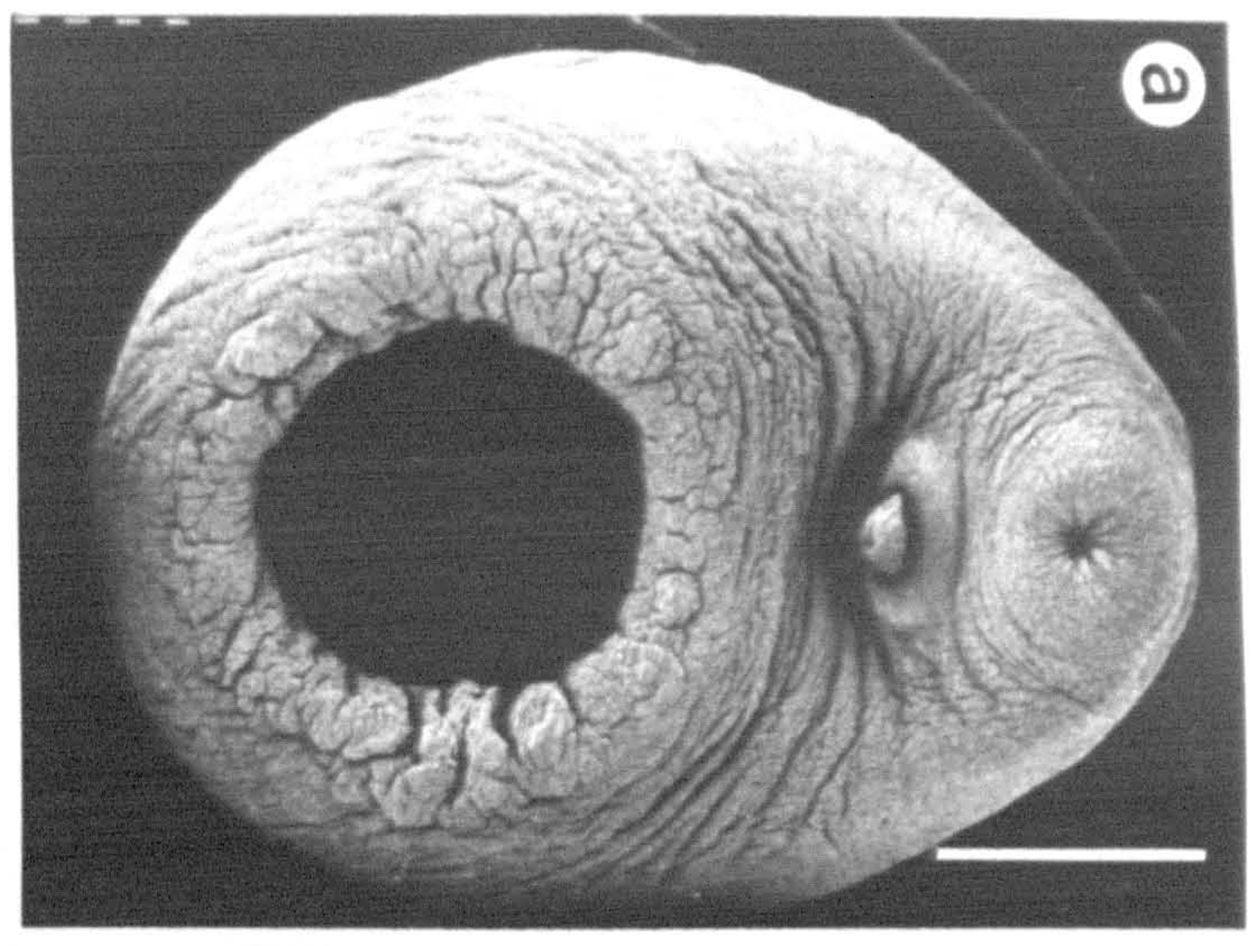
b. Anterior end (scale bar = 200 µm)

c. Genital pore region (scale bar = 200 µm)

d. Internal surface of pharynx, note absence of papillae (scale bar = 100 µm)

e. Acetabular region (scale bar = 200 µm)


d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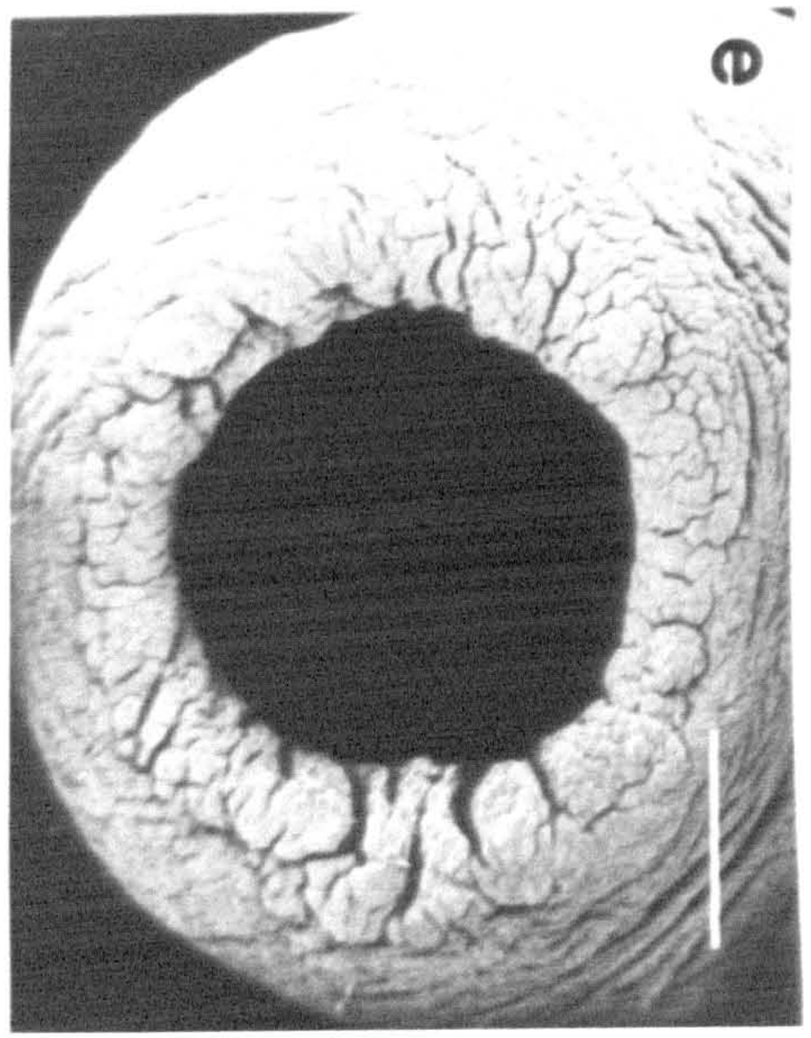
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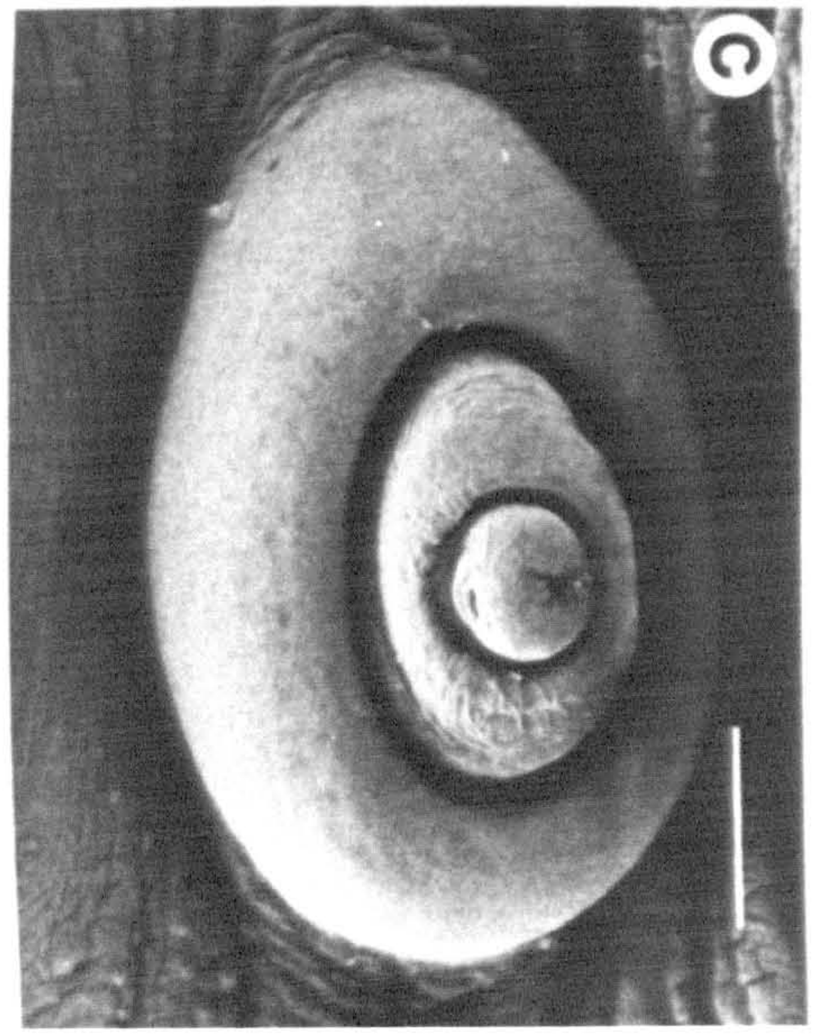
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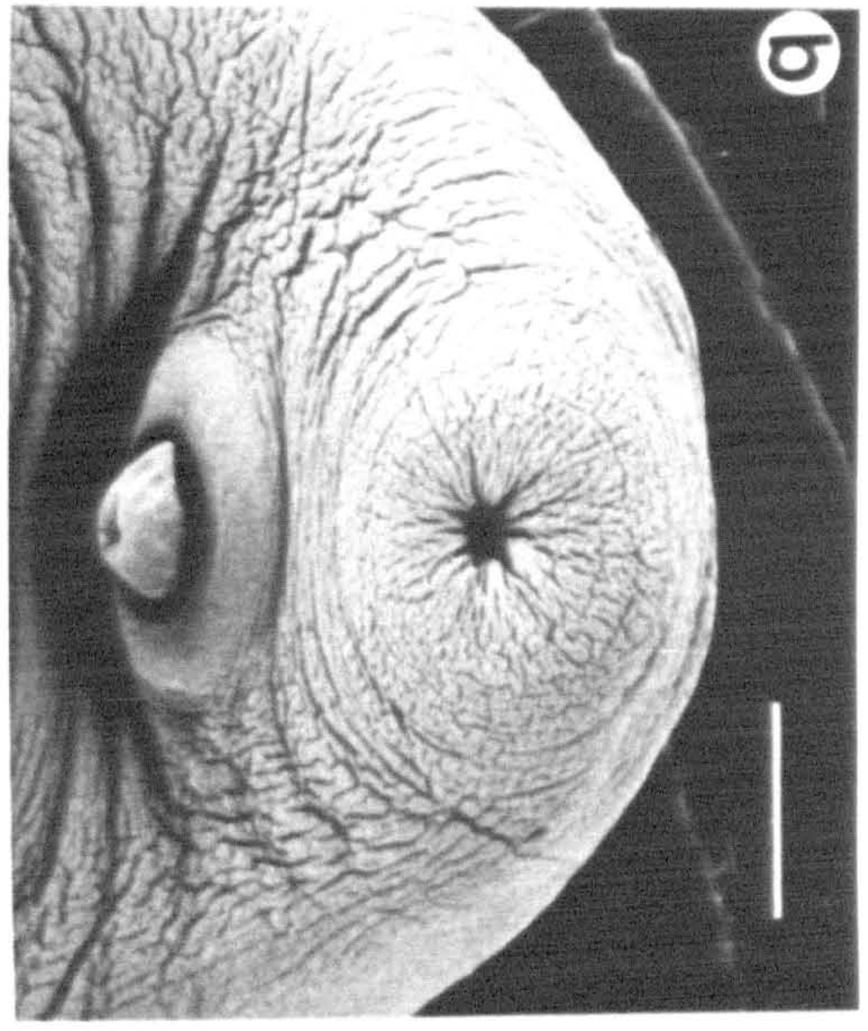

b

FIGURE 104

Gigantocotyle gigantocotyle (Brandes in Otto, 1896)

Näsmark, 1937

a. Whole worm, ventral view

b. Whole worm, sagittal view

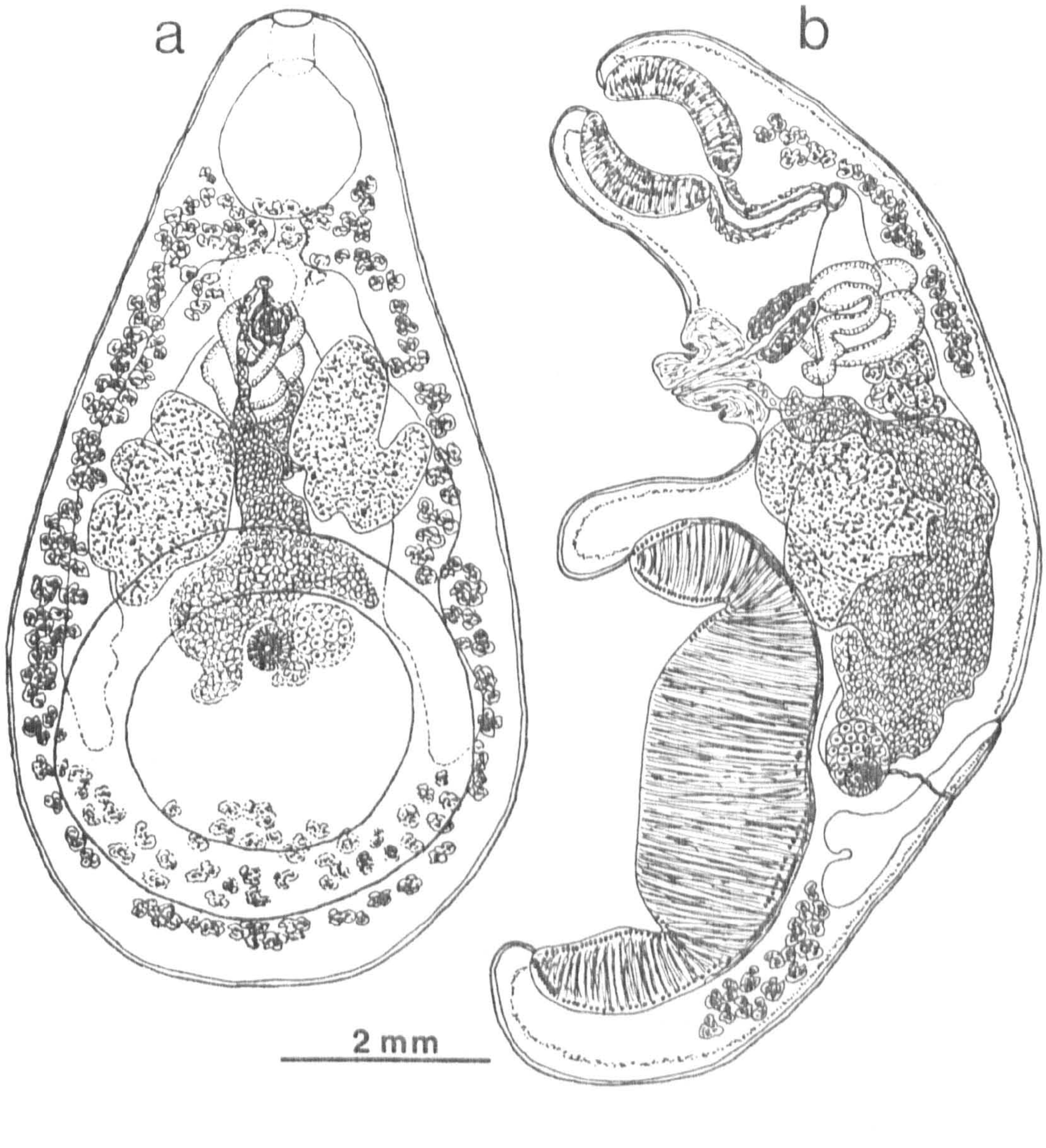

a
b
2 mm

FIGURE 105

Gigantocotyle gigantocotyle (Brandes in Otto, 1896)
Näsmark, 1937
(median sagittal section)

a. Acetabulum (gigantocotyle type)

b. Pharynx (explanatum type) and oesophagus

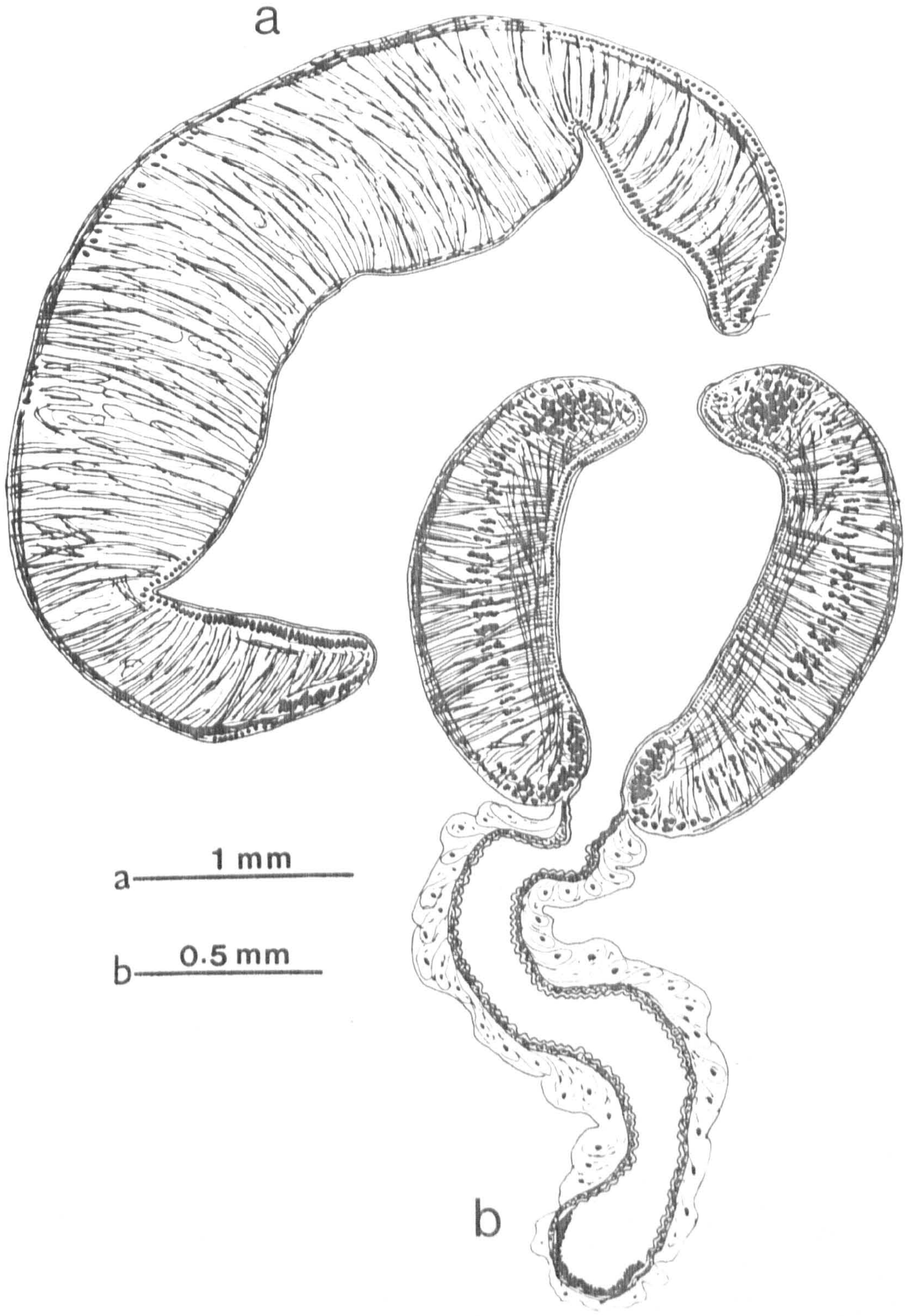

a
1 mm
b
0.5 mm
b

FIGURE 106

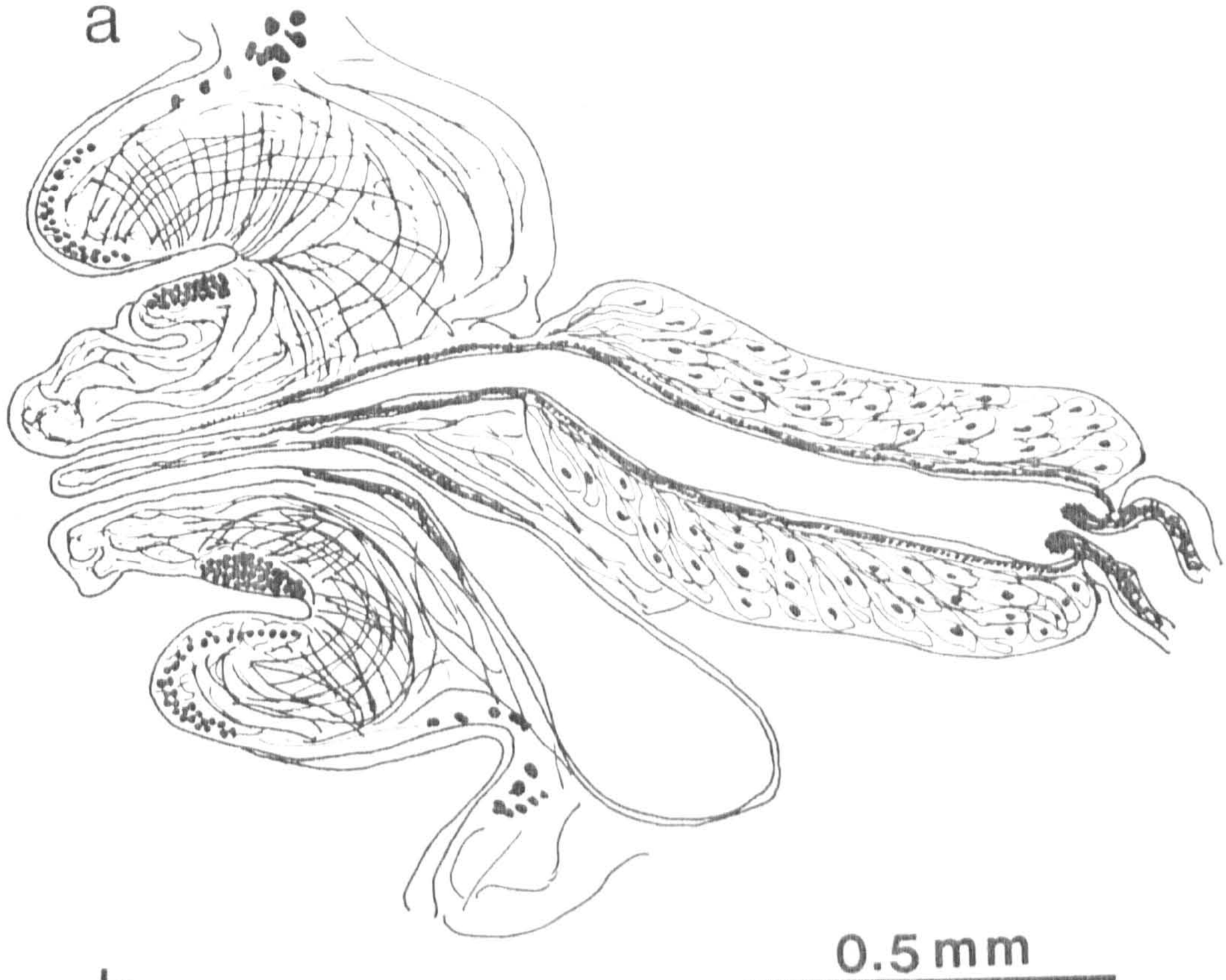
Gigantocotyle gigantocotyle (Brandes in Otto, 1896)
Näsmark, 1937
(median sagittal section)

Various forms of the terminal genitalium (gigantocotyle type) and showing also the pars prostatica

a. Relaxed form

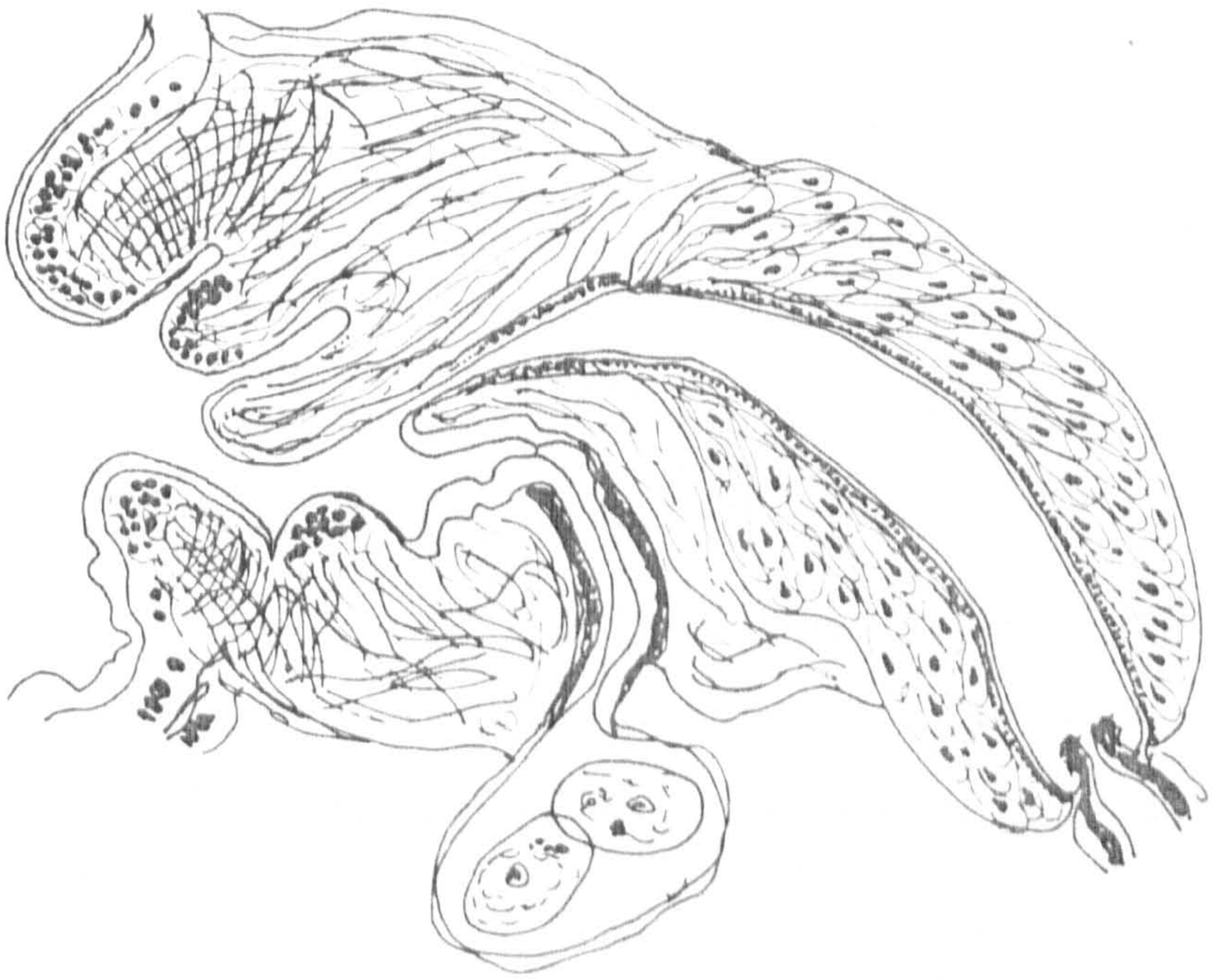
b. Retracted form

a



0.5 mm

b



Gigantocotyle formosanum (Fukui, 1929) Näsmark, 1937

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collection

Bos taurus	Taiwan	Naturhistoriska riksmuseet (Stockholm), Näsmark's material from the original collection of Fukui.
Bubalus bubalis	India	London School of Hygiene & Tropical Medicine coll. no. 830.
	Masbate, Philippines	Author's own collection
	Vietnam	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.

HABITAT: Rumen and Abomasum

DESCRIPTION:

Body pyriform, tapers anteriorly, much broader and rounded posteriorly, curved ventrally, 6.50-9.61 mm long, 3.10-4.82 mm in the dorso-ventral direction. Body surface has tegumental papillae present on anterior part of the body.

Acetabulum subterminal, enormous, 3.01-3.77 mm in external diameter in the dorso-ventral direction; ratio to body length 1:2.1 to 1:2.4; of the symmeri type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 16-22; d.e.c.2, 4-10; d.i.c., 29-36; v.e.c., 12-16; v.i.c., 35-46; m.e.c., 6-9.

Pharynx 0.91-1.15 mm long, 0.72-0.96 mm in the dorso-ventral direction; ratio to body length 1:6.8 to 1:8.5, to the diameter of the acetabulum 1:1.3 to 1:3.8; of the explanatum type (sensu Näsmark, 1937) in median sagittal section; internal surface smooth, devoid of papillae. Oesophagus 0.86-0.93 mm long, musculature of wall relatively thick throughout the length, no bulb or posterior sphincter, lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, nearly straight in their course, reach level of anterior border of acetabulum with the blind ends directed posteriorly.

Testes shallowy lobed, obliquely tandem in middle third of the body; anterior testis 0.92-1.25 mm long, 1.90-2.26 mm in the dorso-ventral direction; posterior testis 0.85-1.13 mm long, 1.83-1.96 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa well developed, thick-walled and convoluted; pars prostatica well developed, about two to three times longer than it is wide (0.55-0.74 mm long and 0.24-0.27 mm wide).

Ovary subspherical, 0.46-0.59 by 0.40-0.62 mm, posterior to testes and dorsal to acetabulum; Mehlis' gland close to ovary, 0.29-0.31 by 0.37-0.40 mm; uterus winds forward dorsal to the testes then ventral to the male ducts; vitellaria in lateral fields, consist of few scattered follicles from level of pharynx to acetabulum, not confluent dorso-medially in the anterior or posterior limits; Laurer's canal crosses excretory vesicle or duct and opens on the dorsal surface about 0.82-0.96 mm posteriorly to the excretory pore; egg 100-120 by 51-78 µm.

Genital pore opens on the ventral surface at a level posterior to the oesophageal bifurcation; terminal genitalium of the microbothrium type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level to the anterior testis and anteriorly to the Laurer's canal opening.

FIGURE 107

Gigantocotyle formosanum (Fukui, 1929) Näsmark, 1937

a. Whole worm, ventral view

b. Whole worm, sagittal view

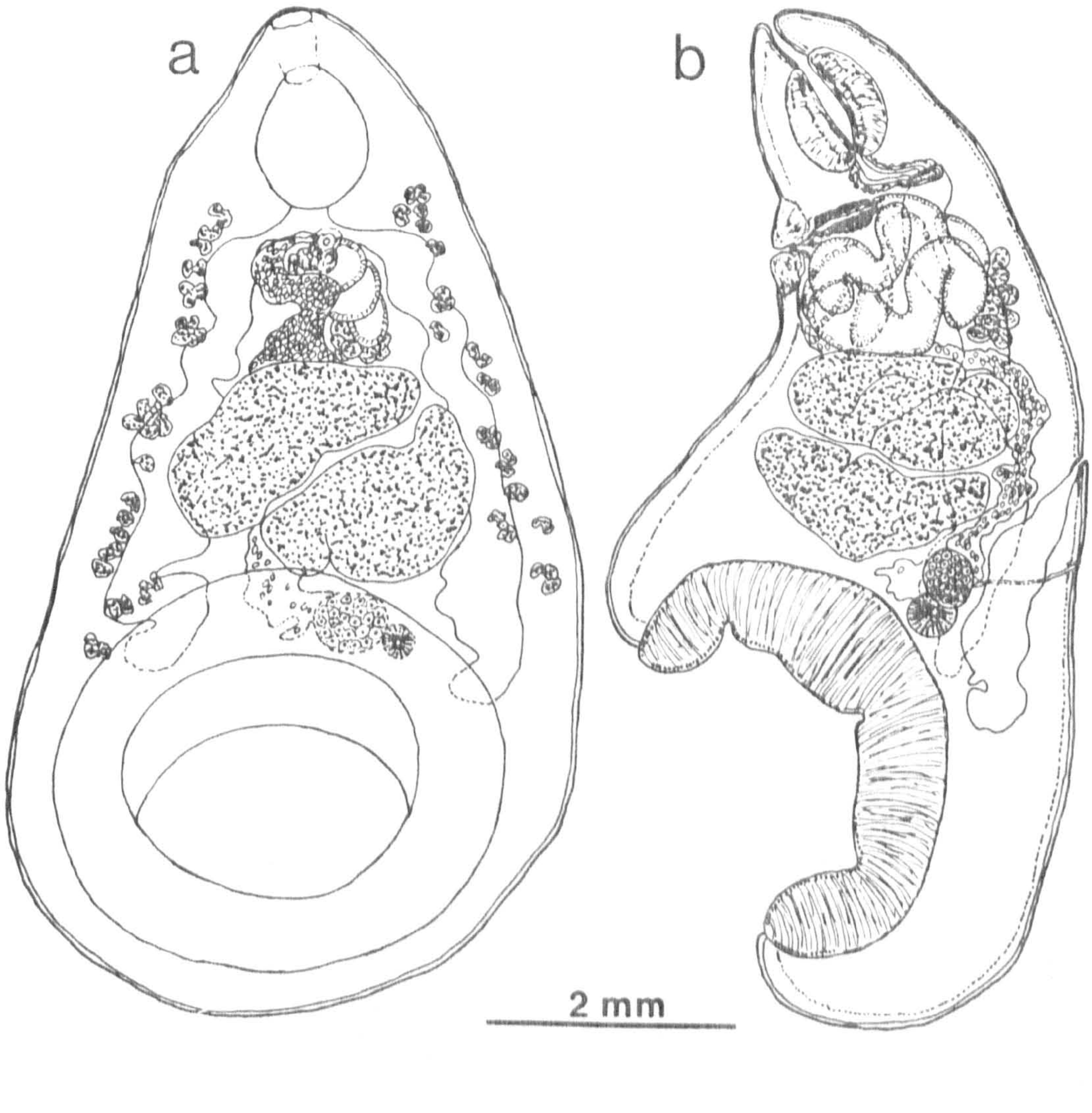

a
b
2 mm

FIGURE 108

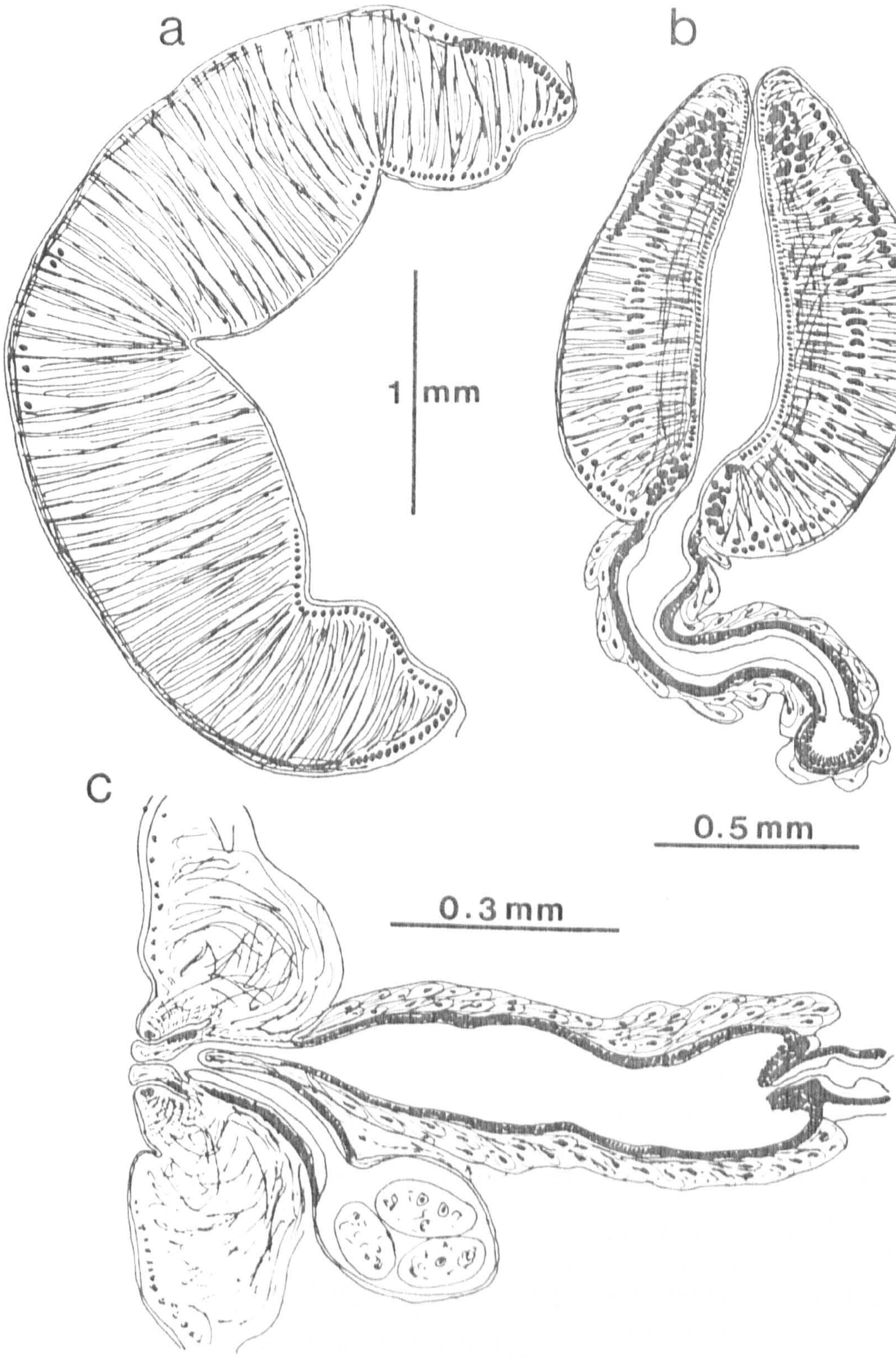
Gigantocotyle formosanum (Fukui, 1929) Näsmark, 1937

(median sagittal section)

a. Acetabulum (symmeri type)

b. Pharynx (explanatum type) and oesophagus

c. Terminal genitalium (microbothrium type) and pars prostatica


a
b
1 mm
C
0.5 mm
0.3 mm

Gigantocotyle symmeri Näsmark, 1937

Synonym: Gigantocotyle lerouxi Yeh, 1957

TYPE SPECIMENS: Naturhistoriska riksmuseet, Stockholm (RMev Sthlm. Coll. No. 2867.1-25) from the rumen of cattle in the Sudan.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collection

Bos indicus	Cameroon	Dr. F. Bertin
Cattle	Khartoum, Sudan	British Museum (Natural History) coll. no. 1957. 12.30.46-57, labeled "P. calicophorum".
	Jonglei, Sudan	Commonwealth Institute of Helminthology coll. no. 44/79.
Kobus leche	Botswana	British Museum (Natural History)
	Zambia	London School of Hygiene & Tropical Medicine
Limnotragus spekei	Zimbabwe	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection, labeled "G. lerouxi".

HABITAT: Rumen, omasum and abomasum

DESCRIPTION:

Body large, tapers anteriorly, broad and rounded posteriorly, strongly curved ventrally, 10.60-13.10 mm long, 5.41-6.03 mm in the dorso-ventral direction. Body surface has large dome-shaped papillae present around the oral opening and ventrally from this point to about the middle of the body.

Acetabulum prominent and enormous, subterminal, 4.20-4.92 mm in external diameter in the dorso-ventral direction; ratio to body length 1:2.4 to 1:2.6; of the symmeri type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 12-18; d.e.c.2, 5-8; d.i.c., 33-42; v.e.c., 14;18; v.i.c., 36-45; m.e.c., 6-10.

Pharynx 1.22-1.55 mm long, 1.21-1.33 mm in the dorso-ventral direction; ratio to body length 1:7.7 to 1:8.2, to the diameter of the acetabulum 1:3.1 to 1:3.5; of the explanatum type (sensu Näsmark, 1937) in median sagittal section; internal surface smooth, devoid of papillae. Oesophagus 0.20-1.21 mm long, musculature of wall relatively thin, no bulb or posterior sphincter; lumen has two kinds of lining, hyaline layer on anterior part and ciliated epithelium on posterior part. Caeca in lateral sides of the body, form dorso-ventral bends during their course, reach level of acetabulum with the blind ends directed postero-ventrally.

Testes deeply lobed, directly tandem in middle third of the body; anterior testis 1.02-1.93 mm long, 2.20-2.48 mm in the dorso-ventral direction; posterior testis 1.18-2.01 mm long; 2.33-2.46 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa well developed, thick-walled and convoluted; pars prostatica well developed, 0.96-1.03 mm long and 0.36-0.51 mm wide.

Ovary subspherical, 0.72-1.15 by 0.80-1.15 mm, dorsal to acetabulum and posterior to testes; Mehlis' gland close to ovary, 0.48-0.82 by 0.62-0.66 mm; uterus winds forward dorsal to testes then ventral to the male ducts; vitellaria in lateral fields,

extend from level of pharynx to posterior border of acetabulum, confluent dorso-medially both in their anterior and posterior limits; Laurer's canal crosses excretory vesicle or duct and opens on the dorsal surface about 1.24-1.50 mm posteriorly to the excretory pore; egg 101-12o by 50-75 µm.

Genital pore opens on the ventral surface at a level posterior to the oesophageal bifurcation; terminal genitalium very prominent, of the gigantocotyle type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level to the posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 109

Gigantocotyle symmeri Näsmark, 1937

(SEM)

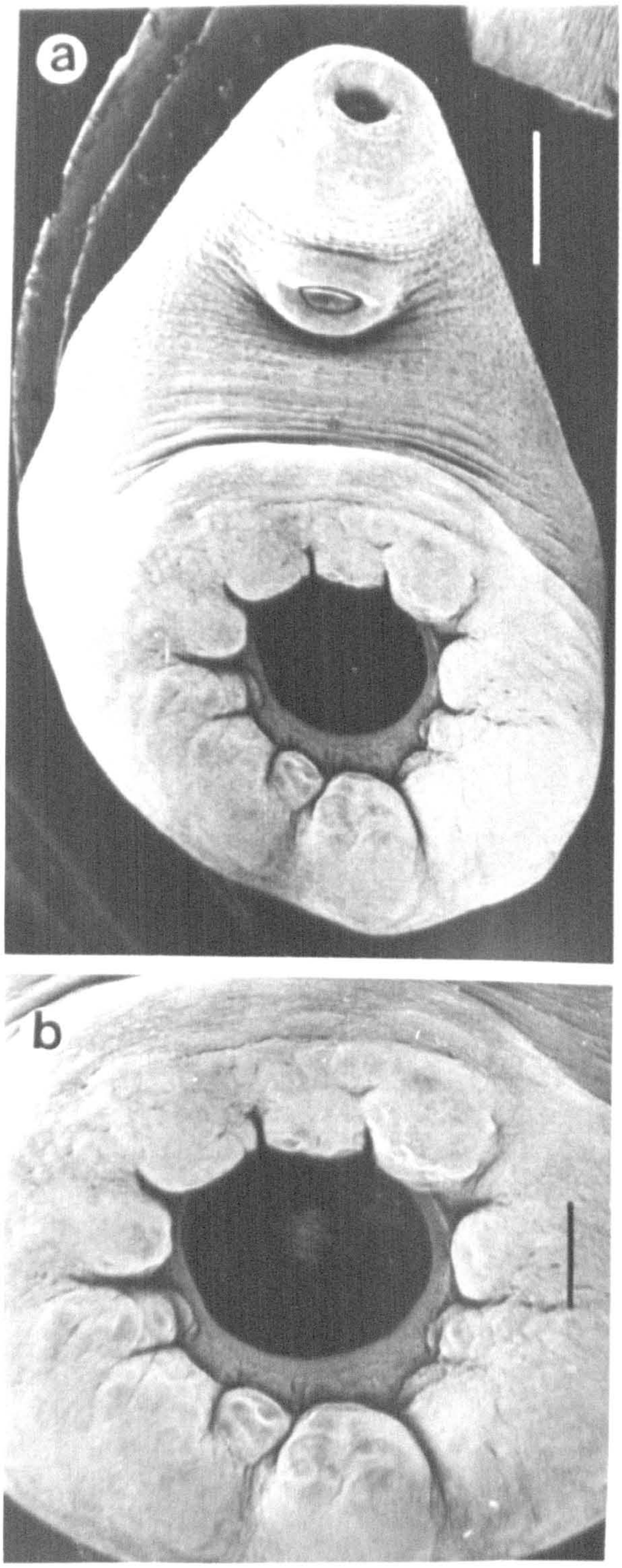
a. Whole worm, ventral view (scale bar = 1 mm)

b. Acetabular region (scale bar = 500 m)

c. Anterior end, note presence of large papillae (scale bar = 20 µm)

d. Closer view of papillae on anterior end, note dome shape (scale bar = 20 µm)

e. Genital pore region (scale bar = 200 µm)


a
b

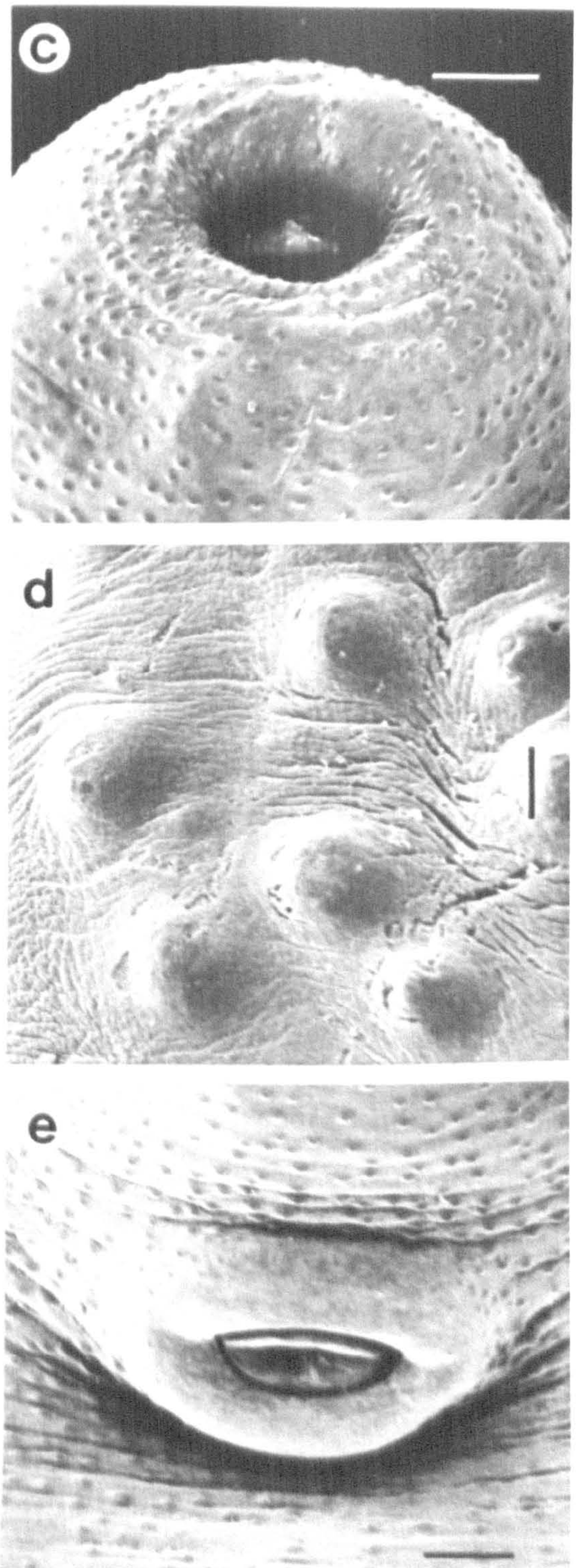

c
d
e

FIGURE 110

Gigantocotyle symmeri Näsmark, 1937

a. Whole worm, ventral view

b. Whole worm, sagittal view

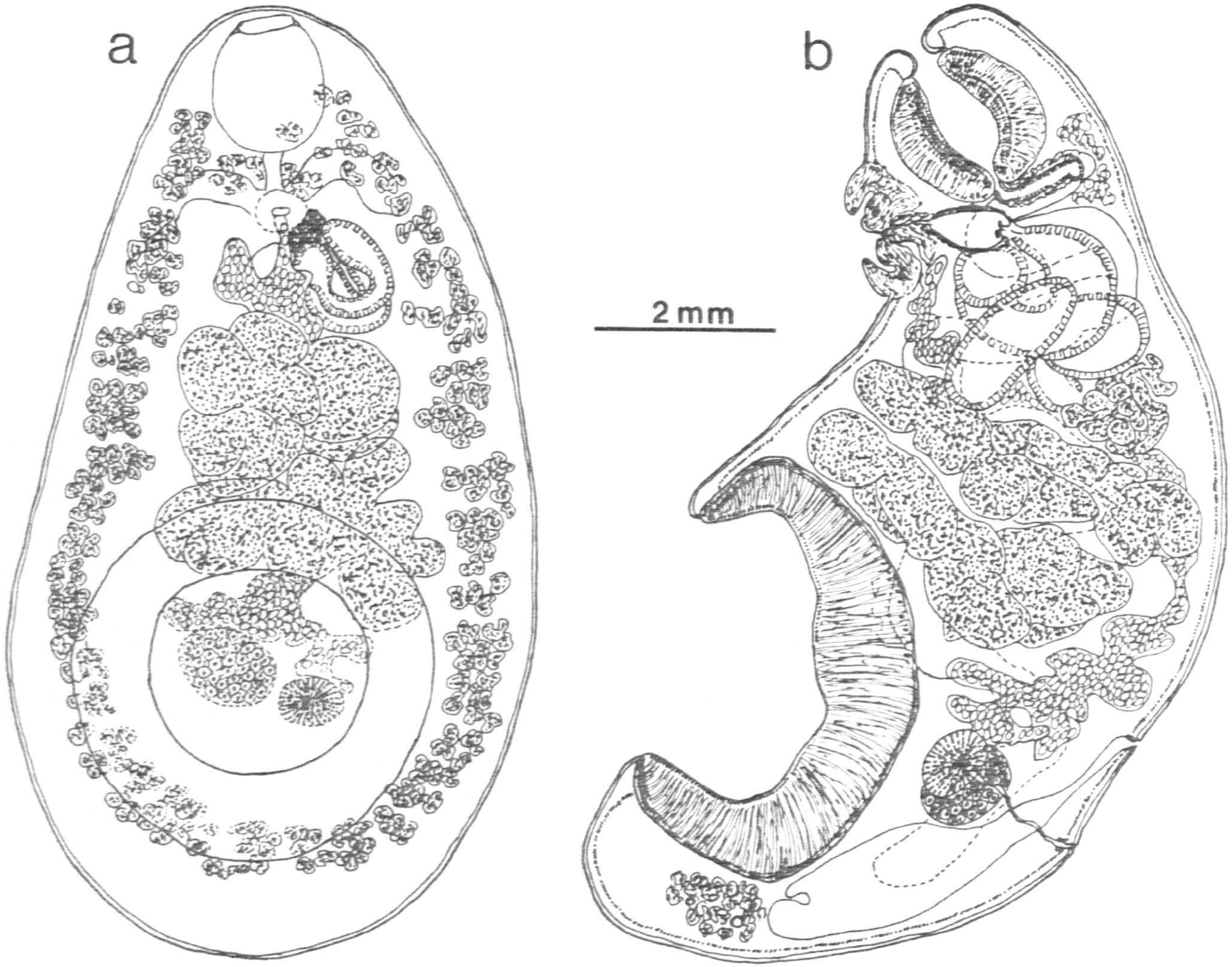

a
b
2 mm

FIGURE 111

Gigantocotyle symmeri Näsmark, 1937

(median sagittal section)

a. Acetabulum (symmeri type)

b. Pharynx (explanatum type) and oesophagus. Note two kinds of lining on lumen of oesophagus, hyaline layer on anterior part and ciliated epithelium on posterior part.

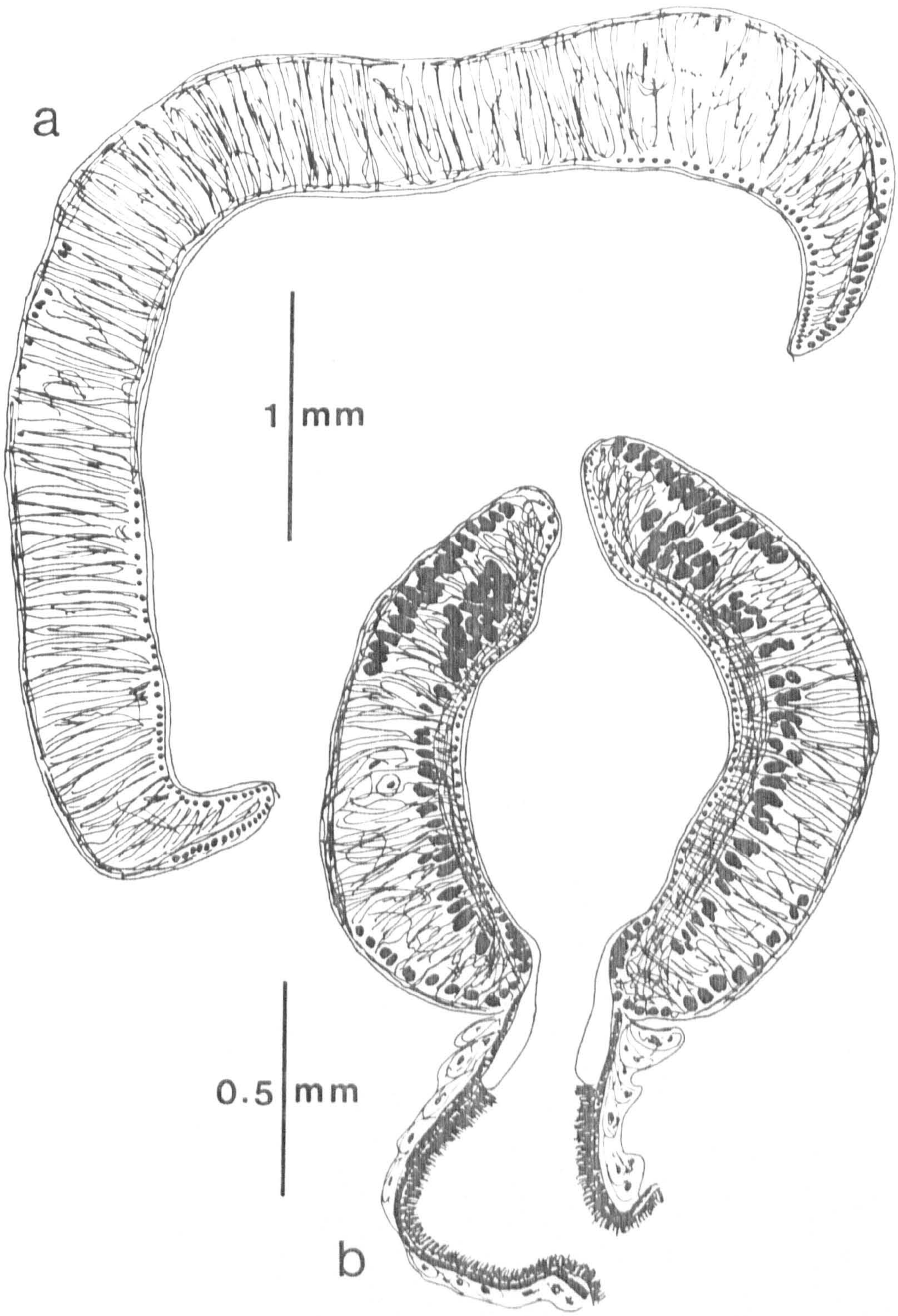
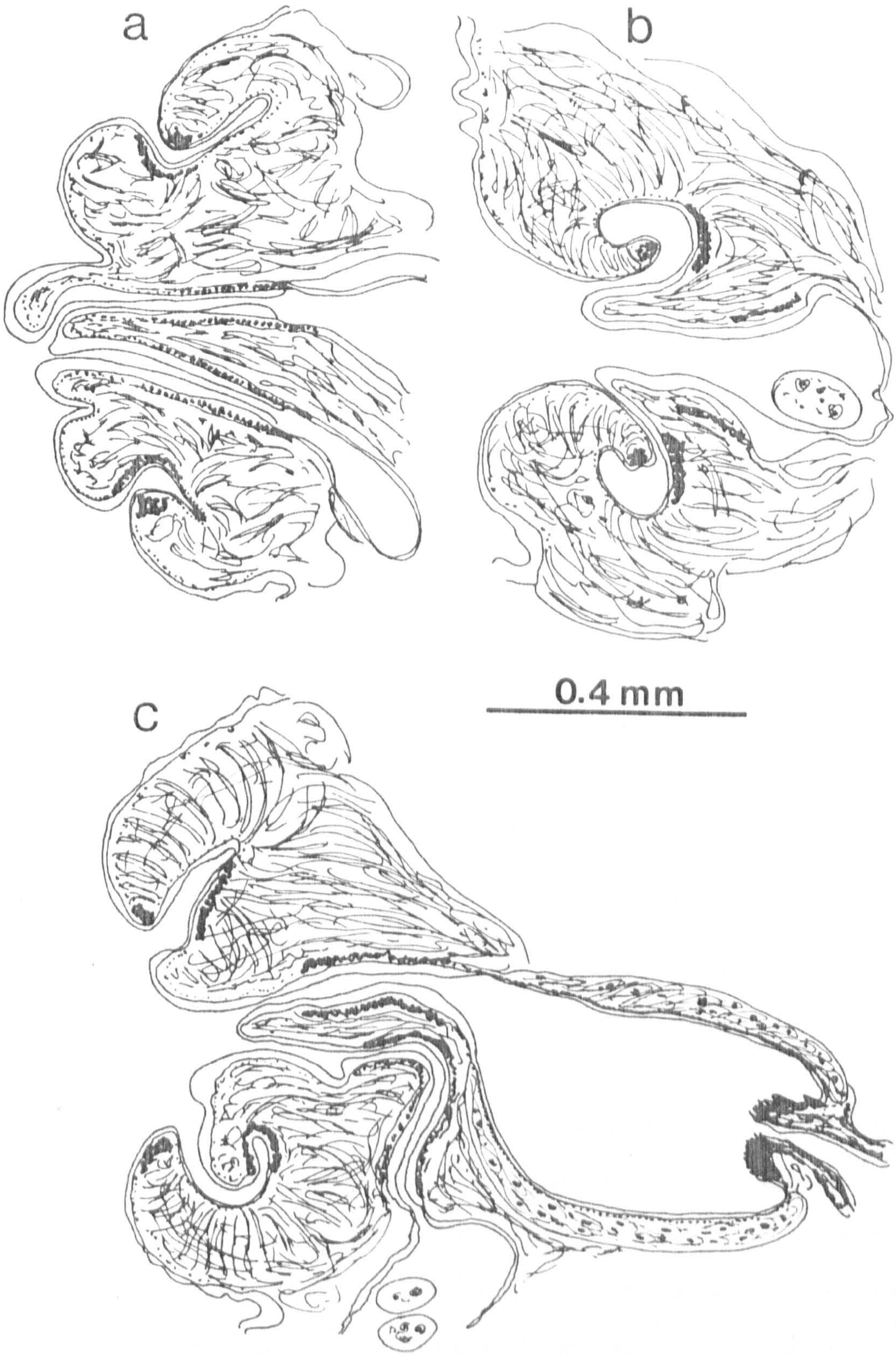

a
1 mm
0.5 mm
b

FIGURE 112

Gigantocotyle symmeri Näsmark, 1937

(median sagittal section)

a - c. Terminal genitalium (gigantocotyle type), various forms at different degrees of relaxation.


a
b
c
0.4 mm

Gigantocotyle duplicitestorum Näsmark, 1937

TYPE SPECIMENS: Naturhistoriska riksmuseet, Stockholm (RMev. Sthlm. Coll. No. JF.1-4, PP.1-4) from the stomach of Hippopotamus amphibius at Kaka, Sudan.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collection

Hippopotamus amphibius	Queen Elizabeth Park, Uganda	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Chinsali and Chambesi Rivers, Zambia	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.

HABITAT: Stomach and small intestine

DESCRIPTION:

Body large, tapers anteriorly, broad and rounded posteriorly, curved ventrally, 8.43-9.51 mm long, 3.22-4.63 mm in the dorsao-ventral direction. Body surface lacks tegumental papillae.

Acetabulum subterminal, enormous, e.00-4.09 mm in external diameter in the dorso-ventral direction; ratio to body length 1:2 to 1:2.5; of the duplicitestorum type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 15-20; d.e.c.2, 23-26; d.i.c., 35-44; v.e.c., 10-16; v.i.c., 34-39; m.e.c., absent.

Pharynx 1.05-1.52 mm long, 0.78-1.12 mm in the dorso-ventral direction; ratio to body length 1:5.8 to 1:8.6, to the diameter of the acetabulum 1:3 to 1:3.4; of the explanatum type (sensu Näsmark, 1937) in medisan sagittal section; internal surface smooth, devoid of papillae. Oesophagus 0.56-0.98 mm long, musculature of wall uniformly thick, no bulb or posterior sphincter; lumen lined by hyalinelayer throughout its length. Caeca in lateral sides of the

body, nearly straight in their course, reach level of acetabulum on its dorsal side with the blind ends directed medially.

Testes indented, tandem in middle third of the body; anterior testis 0.70-0.89 mm long, 1.38-2.34 mm in the dorso-ventral direction; posterior testis 0.66-0.82 mm long, 1.90-2.08 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa well developed, thick-walled and convoluted; pars prostatica well developed, about two to three times longer than it is wide (0.35-0.58 mm long, 0.13-0.20 mm wide).

Ovary subspherical, 0.50-0.62 by 0.47-0.51 mm, posterior to testes and dorsal to acetabulum; Mehlis' gland close to ovary, 0.23-0.39 by 0.35-0.36 mm; uterus winds forward dorsal to testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of pharynx to acetabulum, not confluent dorso-medially in their anterior or posterior limits; Laurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface about 0.70-0.93 mm posteriorly to the excretory pore; egg 140-153 by 75-78 µm.

Genital pore opens on the ventral surface at level of the oesophagus or its bifurcation; terminal genitalium of the microbothrium type (sensu Näsmark, 1937) but small and not prominent.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface at the level of the posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 113

Gigantocotyle duplicitestorum Näsmark, 1937

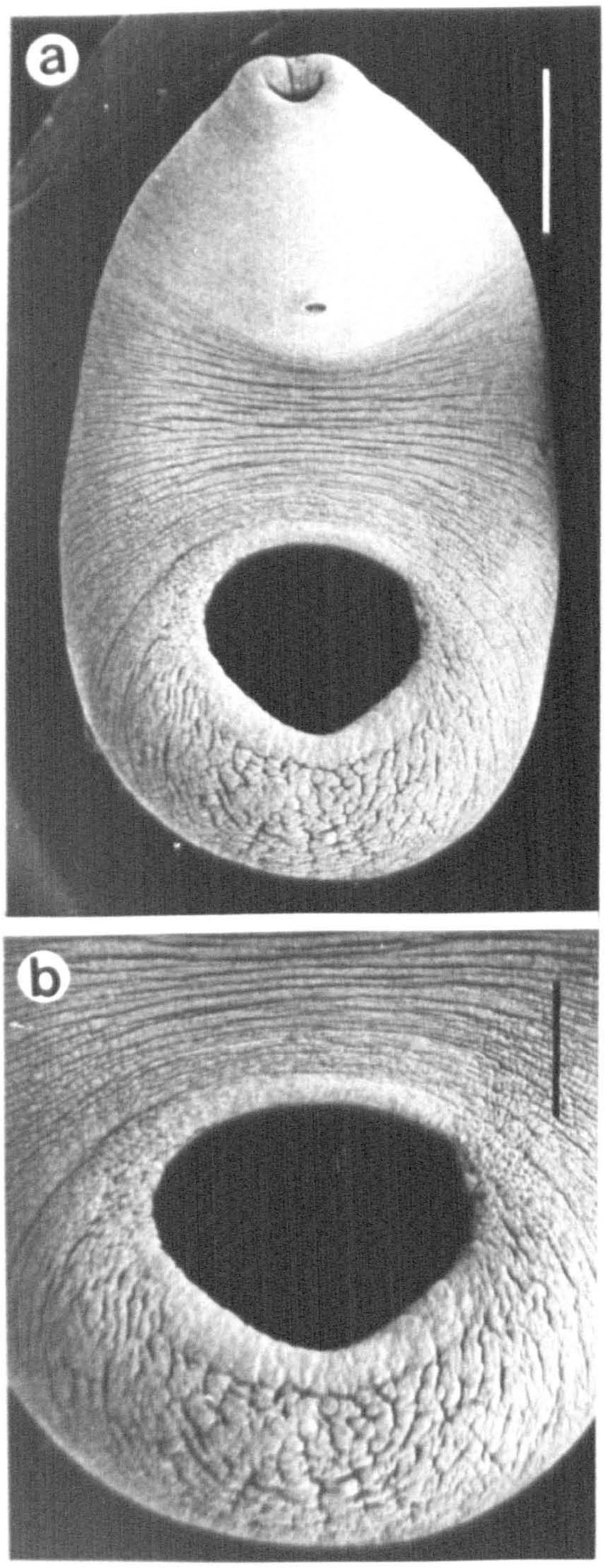
(SEM)

a. Whole worm, ventral view (scale bar = 1 mm)

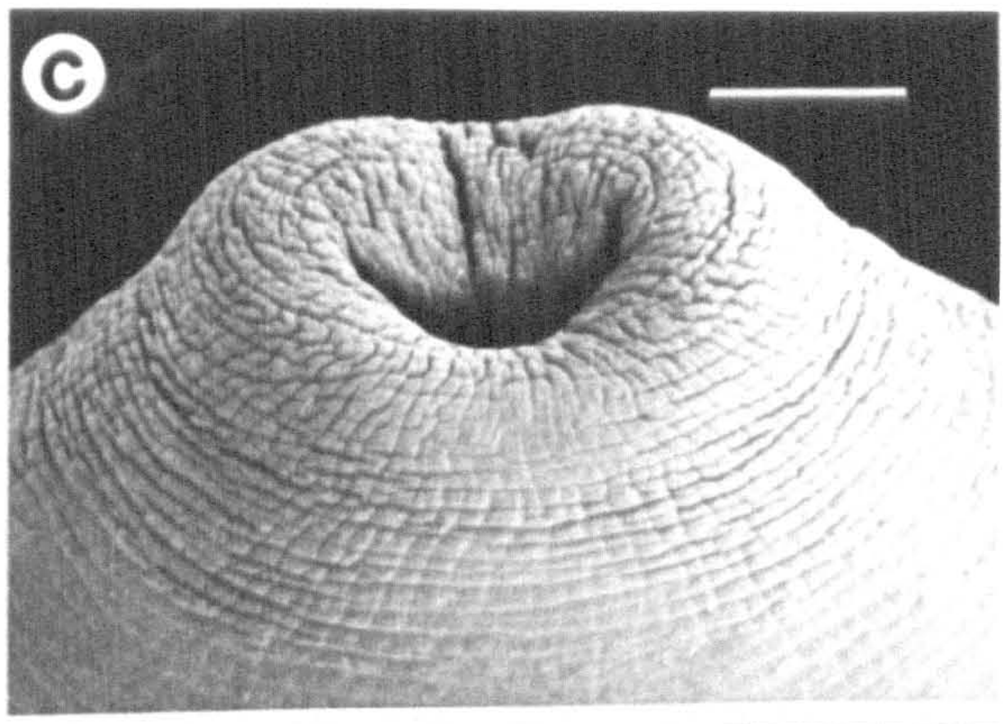
b. Acetabular region (scale bar = 1 mm)

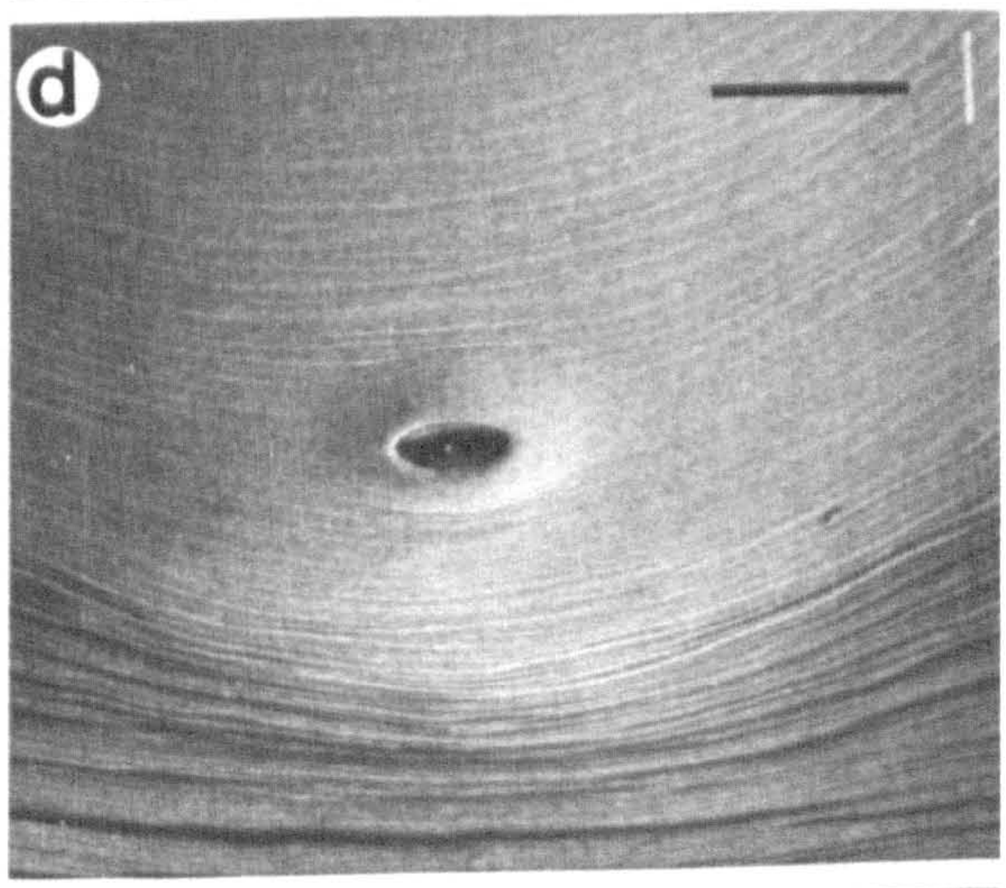
c. Genital pore region (scale bar = 200 µm)

d. Another genital pore region (scale bar = 200 µm)


a

b


c


d

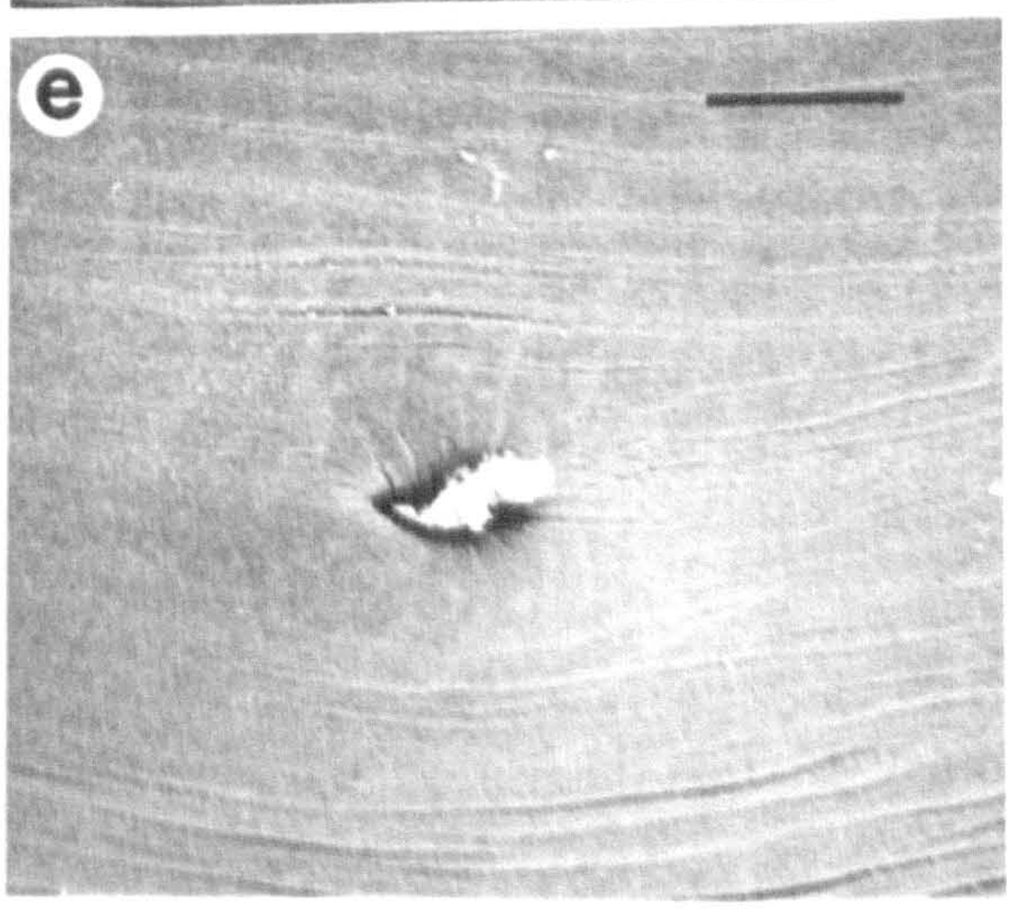

e

FIGURE 114

Gigantocotyle duplicitestorum Näsmark, 1937

a. Whole worm, ventral view

b. Whole worm, sagittal view

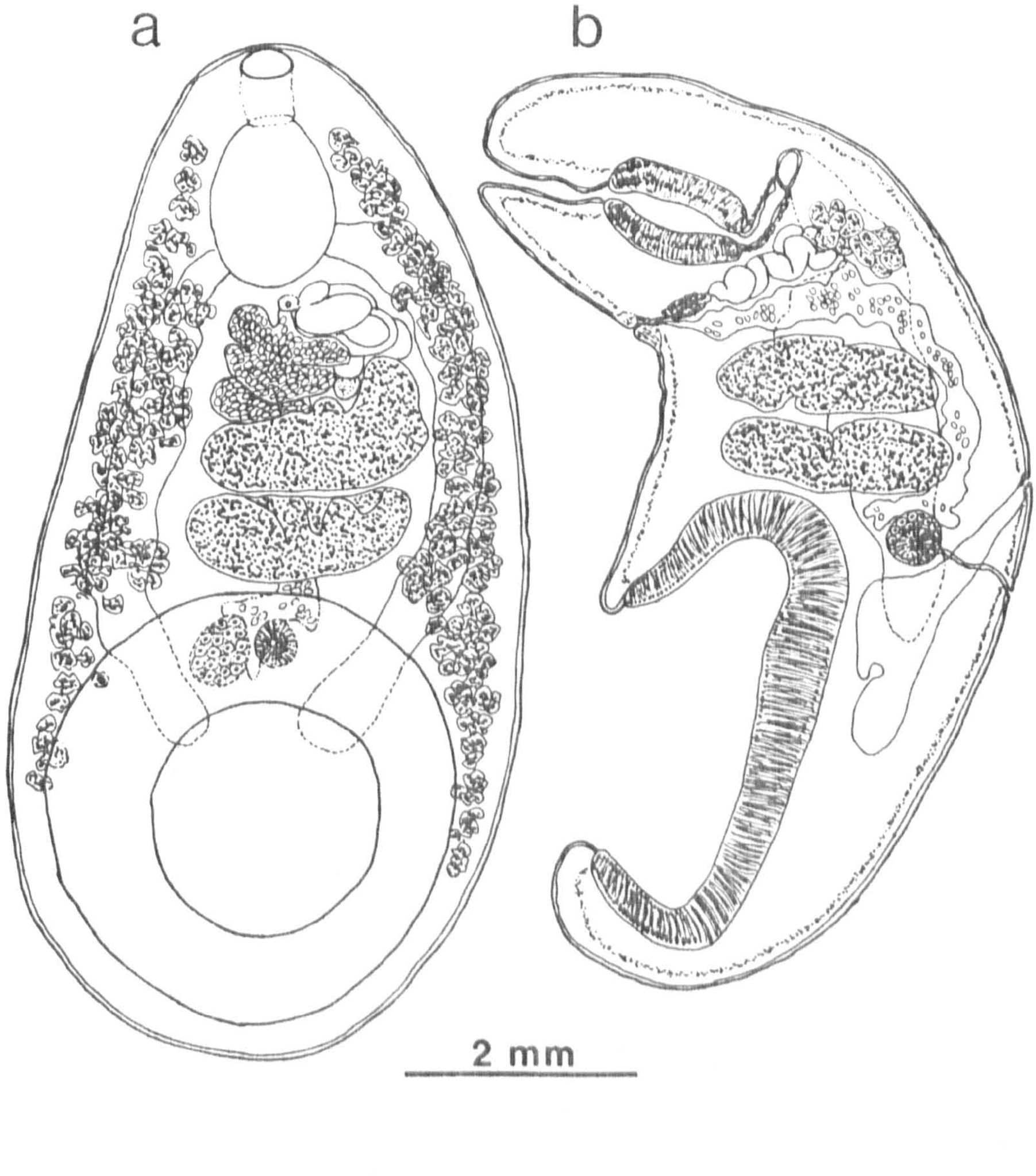

a
b
2 mm

FIGURE 115

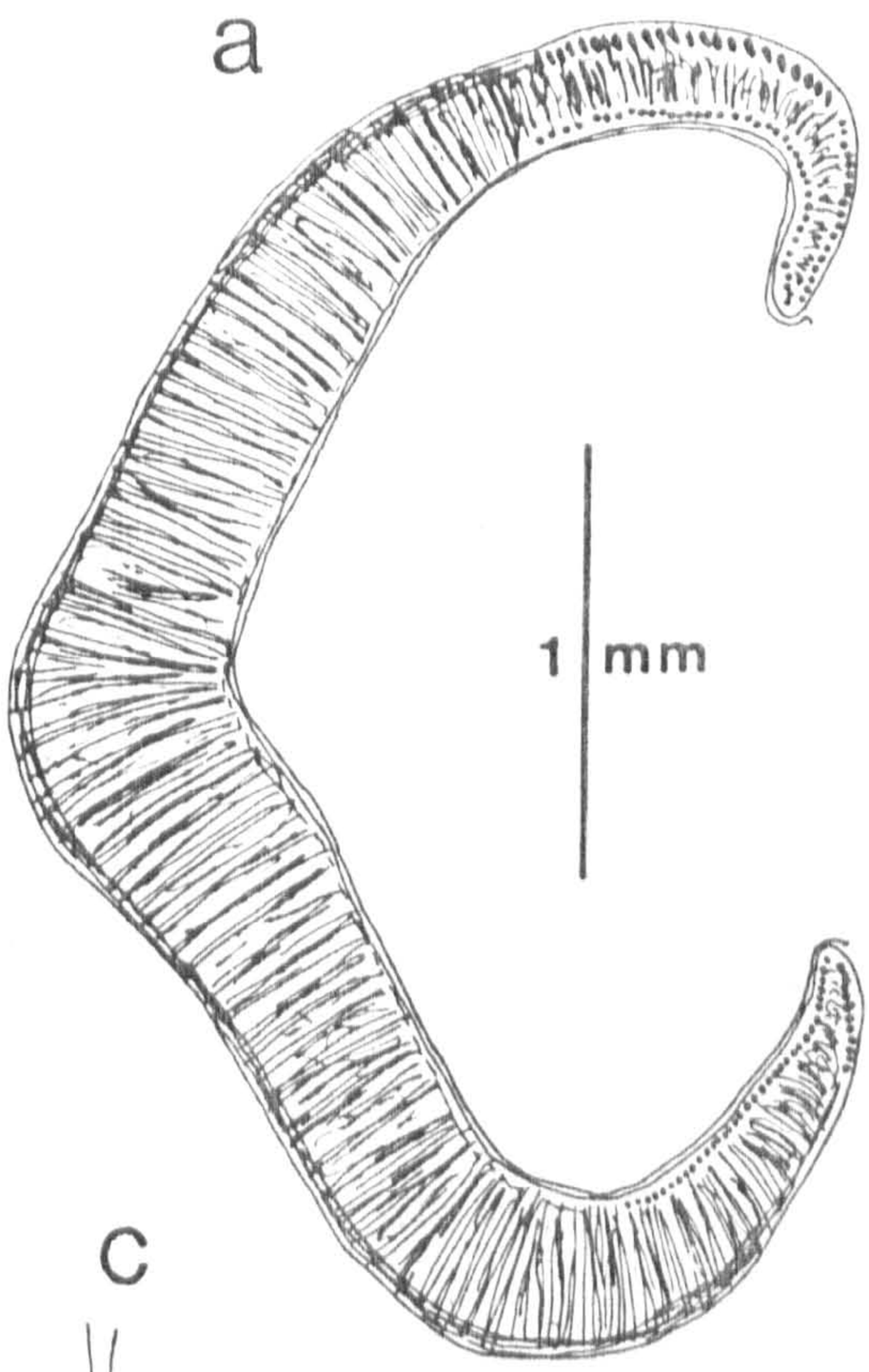
Gigantocotyle duplicitestorum Näsmark, 1937

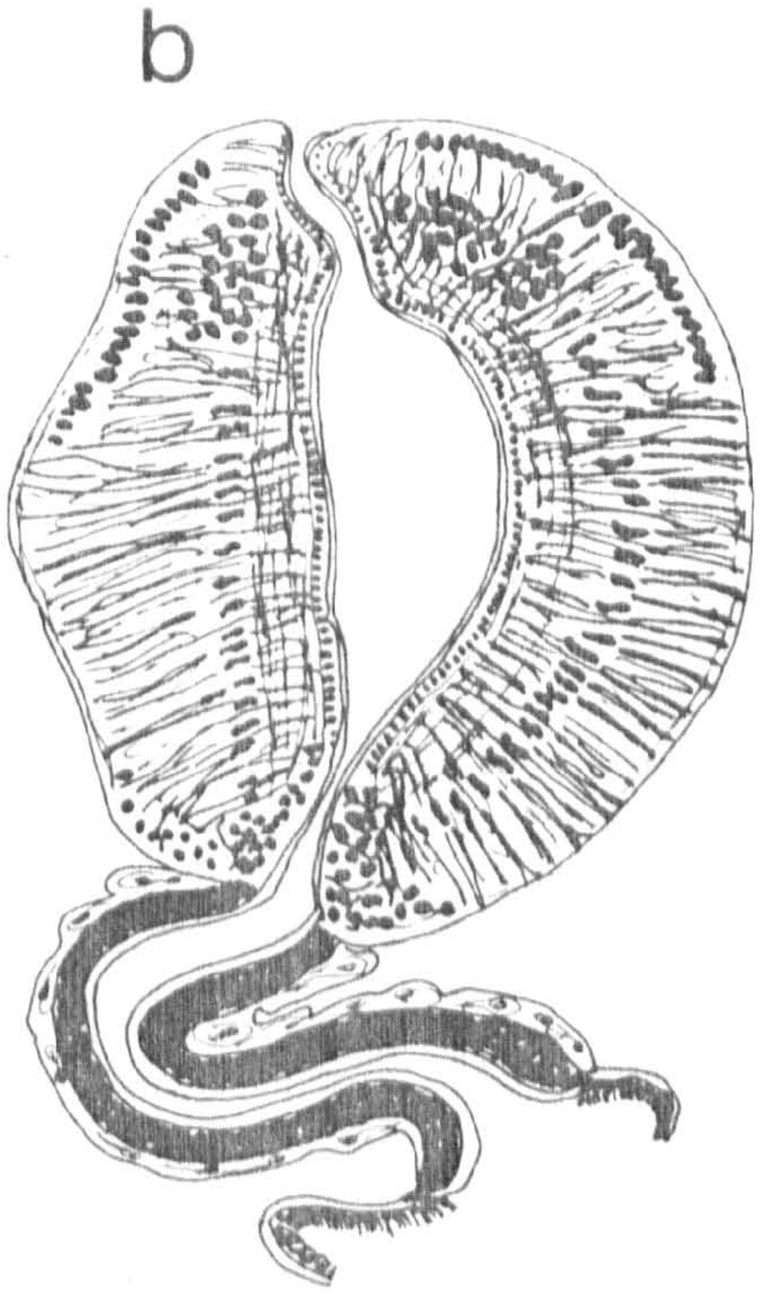
(median sagittal section)

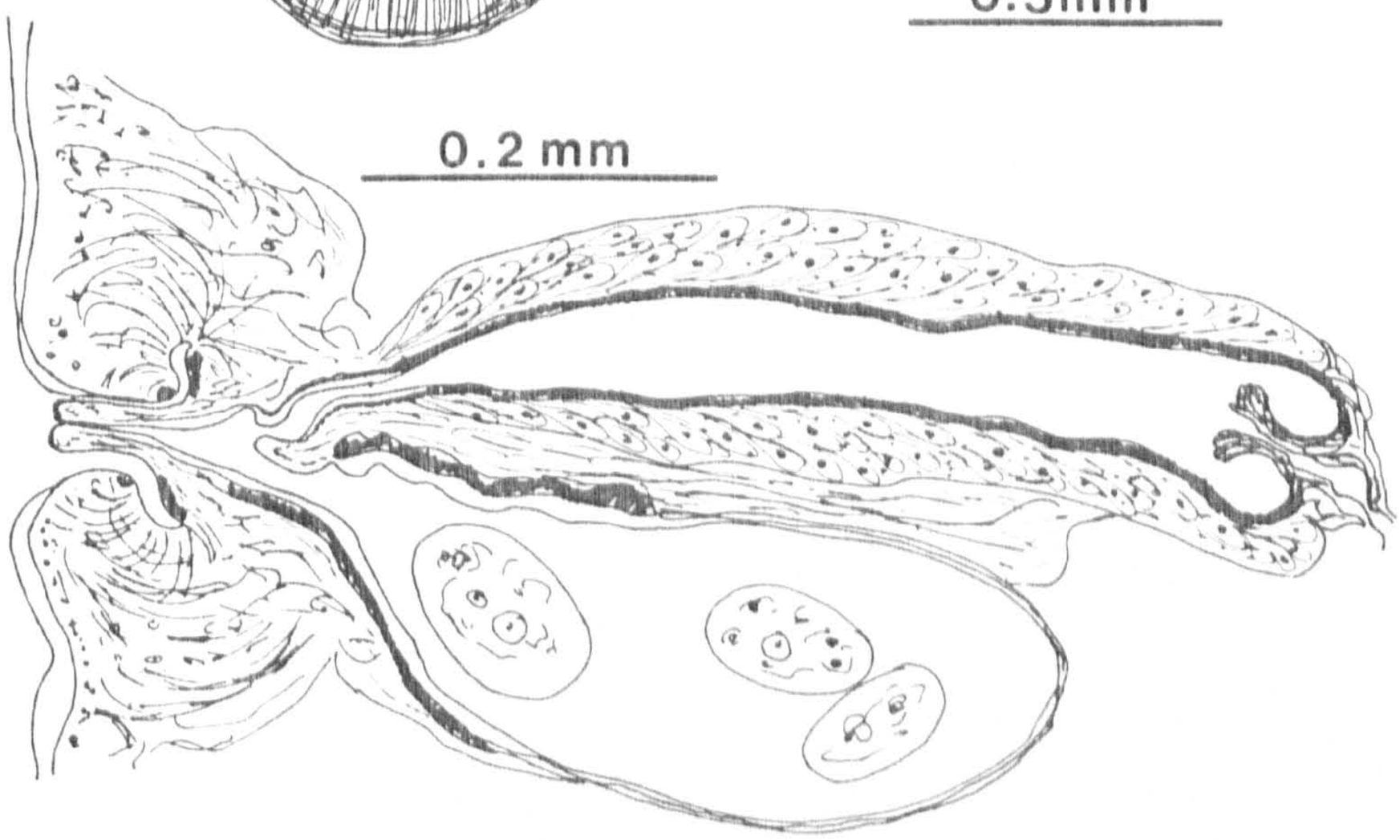
a. Acetabulum (duplicitestorum type)

b. Pharynx (explanatum type) and oesophagus

c. Terminal genitalium (microbothrium type) and pars prostatica


a
1 mm


b
0.5mm


C
0.2 mm

Explanatum Fukui, 1929 status emended

GENERIC DIAGNOSIS

Paramphistomidae, Paramphistominae. Body small to large and conical, curved ventrally, round to oval in cross section; ventral pouch absent. Acetabulum enormous in size and subterminal. Pharynx without pouch or diverticle; oesophagus without bulb or posterior sphincter; caeca in lateral sides of the body, straight or sinuous in their course, reach level of acetabulum. Testes lobed, directly or obliquely tandem; seminal vesicle long, thin-walled and deeply coiled; pars musculosa very short and weakly developed; pars prostatica moderately to weakly developed. Ovary and Mehlis' gland posttesticular; Laurer's canal crosses the excretory vesicle or duct; vitellaria in lateral fields, not confluent dorso-medially in their anterior or posterior limits. Genital sucker absent. Parasitic in the bile duct and liver of ruminants.

Type species: Explanatum explanatum (Creplin, 1847) Fukui, 1929

Explanatum explanatum (Creplin, 1847) Fukui, 1929

Synonyms: Paramphistomum fraternum Stiles and Goldberger, 1910
Paramphistomum siamense Stiles and Goldberger, 1910

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collections

Bubalus bubalis	India	London School of Hygiene & Tropical Medicine coll. no. 819.
	Sri Lanka	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Buffalo	Afghanistan	Commonwealth Institute of Helminthology
	India	London School of Hygiene & Tropical Medicine coll. no. 826, 711.
Goat	Iraq	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.

HABITAT: Liver, gall bladder and bile ducts

DESCRIPTION:

Body large, tapers anteriorly, broad and rounded posteriorly, curved ventrally, 7.86-14.30 mm long, 3.75-5.38 mm in the dorso-ventral direction. Body surface has papillae on its anterior part around the oral opening and ventrally from this point to about the middle of the body.

Acetabulum subterminal, enormous, 3.50-4.82 mm in external diameter in the dorso-ventral direction; ratio to body length 1:2.2 to 1:3.5; of the explanatum type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 10-15; d.e.c.2, 20-38; d.i.c., 40-51; v.e.c., 10-14; v.i.c., 33-48;

m.e.c., 3-9.

Pharynx 0.75-1.09 mm long, 0.78-0.88 in the dorso-ventral direction; ratio to body length 1:8 to 1:8.8, to the diameter of the acetabulum 1:3.6 to 1:5.5; of the explanatum type (sensu Näsmark, 1937) in median sagittal section; internal surface smooth, devoid of papillae. Oesophagus 0.85-0.94 mm long, may bend dorsally; musculature of wall relatively thick and more or less uniform in thickness throughout its length, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, slightly wavy dorso-ventrally in their course, procedd posteriorly gradually towards the dorsal side of the body so that the blind ends are directed medially and dorsally to the acetabulum.

Testes slightly lobed, obliquely tandem in middle two third of the body; anterior testis 1.20-1.56 mm long, 1.32-2.65 mm in the dorso-ventral direction; posterior testis 1.33-1.64 mm long; 2.01-2.59 mm in the dorso-ventral direction; seminal vesicle moderate in length, thin-walled and strongly coiled; pars musculosa short and weakly developed; pars prostatica relatively small, 0.16-0.22 mm long and 0.15-0.18 mm wide.

Ovary subspherical, 0.40-0.56 by 0.45-0.50 mm, dorsal to acetabulum, posterior to testes and ventro-lateral to the excretory vesicle; Mehlis' gland close to ovary, 0.32-0.37 by 0.25-0.37 mm; Laurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface about 0.52-0.93 mm posteriorly to the excretory pore; uterus winds forward dorsal to the testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of

pharynx to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 115-125 by 75-79 µm.

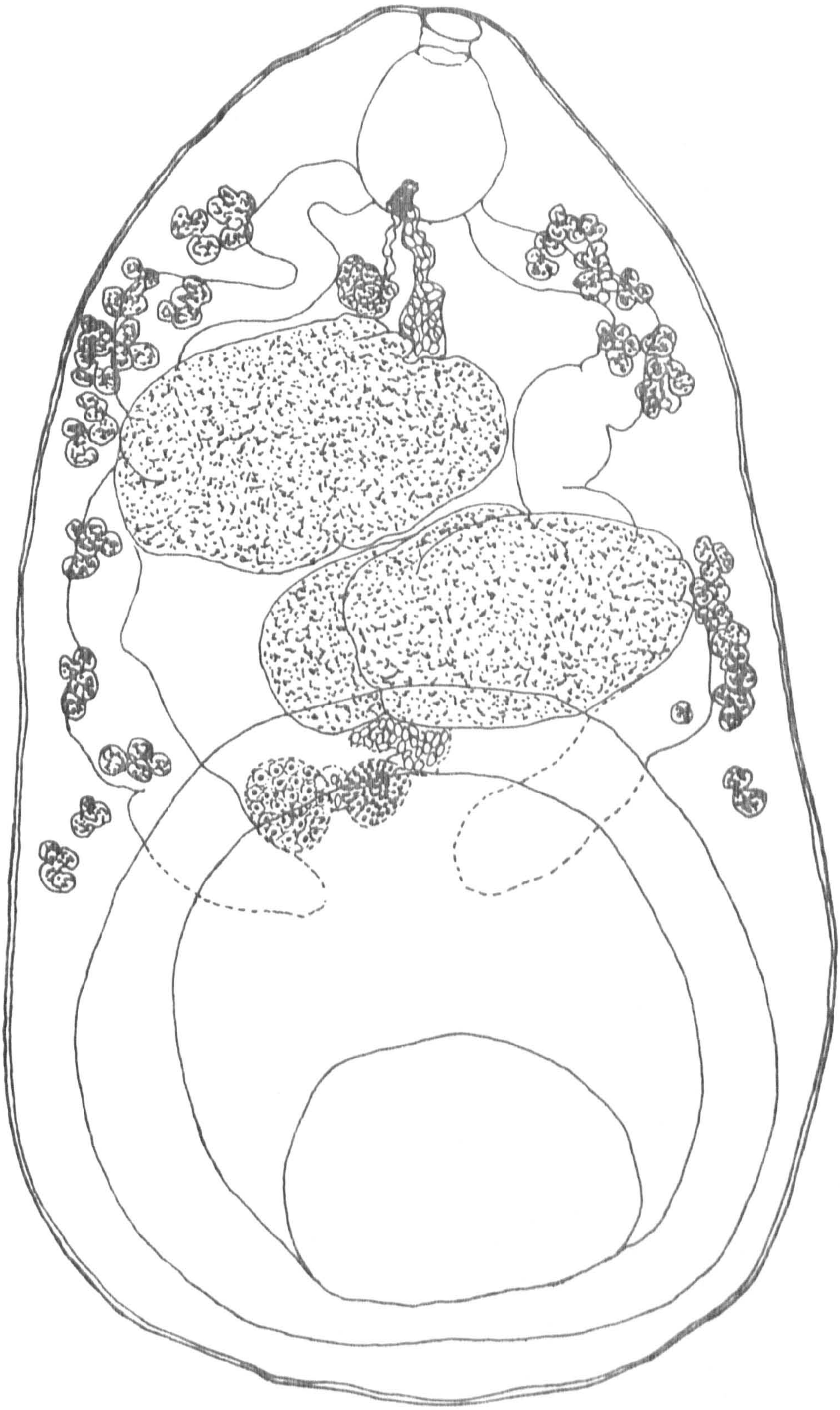
Genital pore opens on the dorsal surface at level of the pharynx or oesophagus; terminal genitalium of the explanatum type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum and medial to ovary and Mehlis' gland; excretory pore opens on the dorsal surface anteriorly to the Laurer's canal opening.

FIGURE 116

Explanatum explanatum (Creplin, 1847) Fukui, 1929

Whole worm, ventral view



2 mm

FIGURE 117

Explanatum explanatum (Creplin, 1847) Fukui, 1929

Whole worm, sagittal view

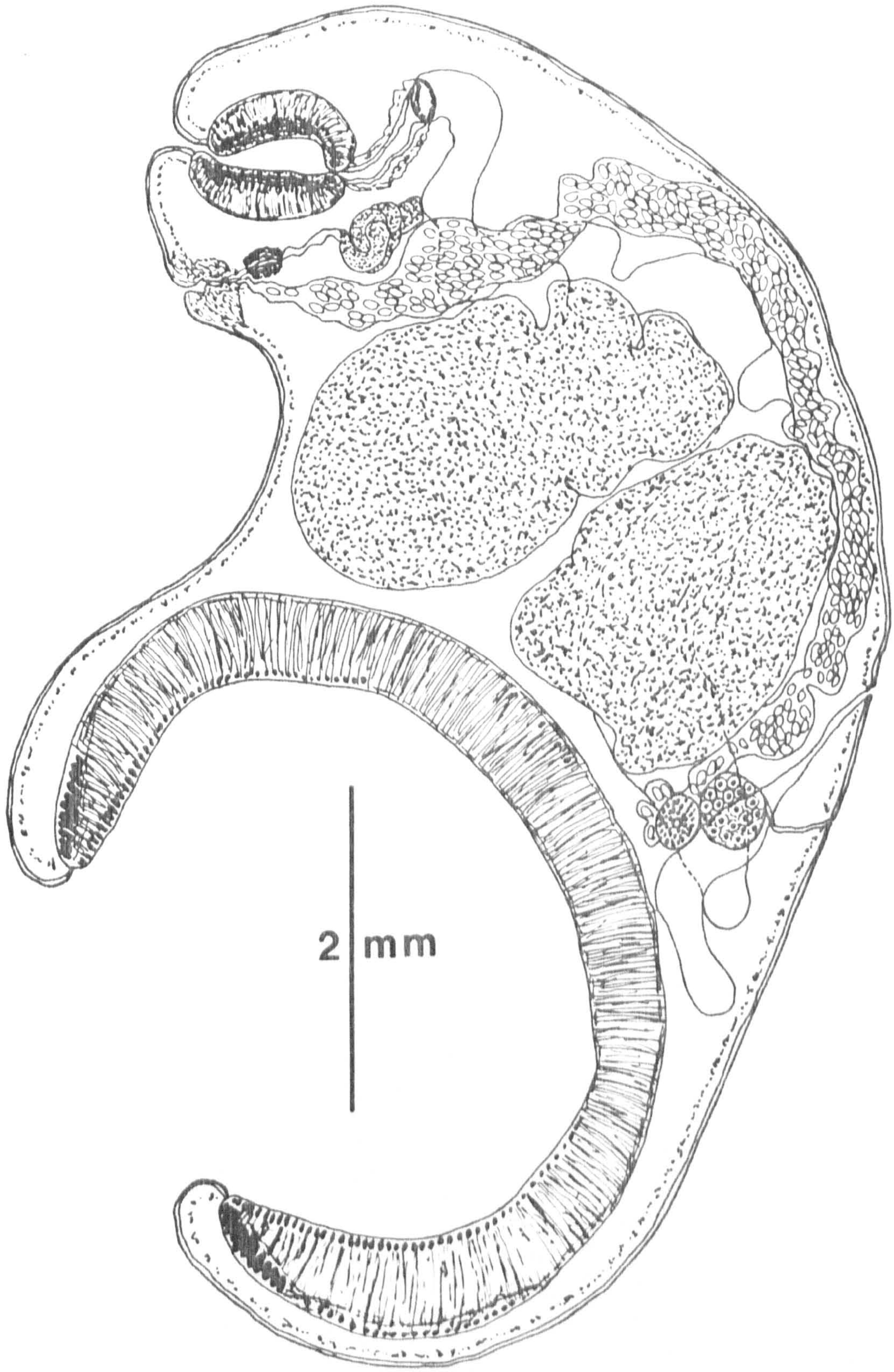

2 mm

FIGURE 118

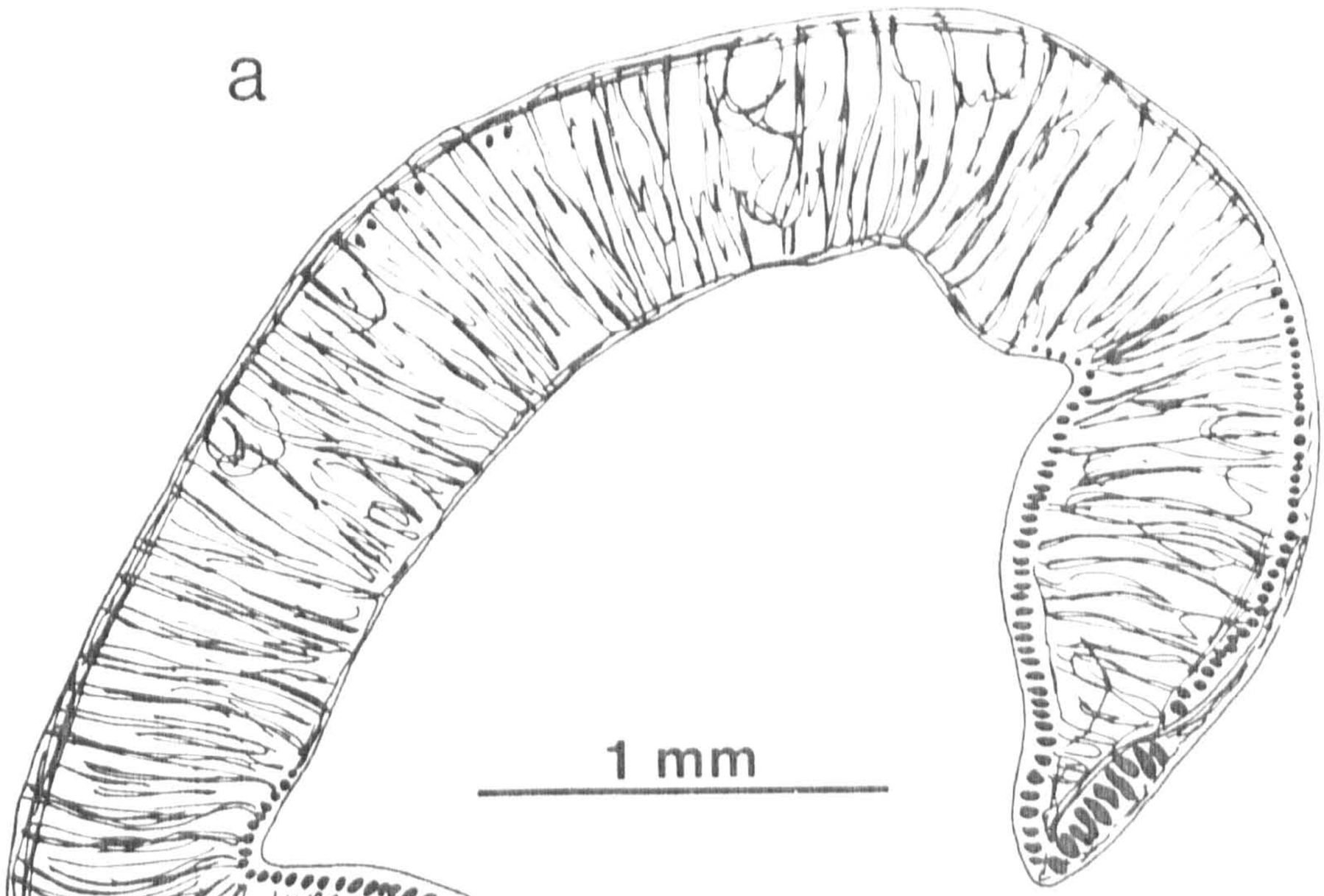
Explanatum explanatum (Creplin, 1847) Fukui, 1929

(median sagittal setion)

a. Acetabulum (explanatum type)

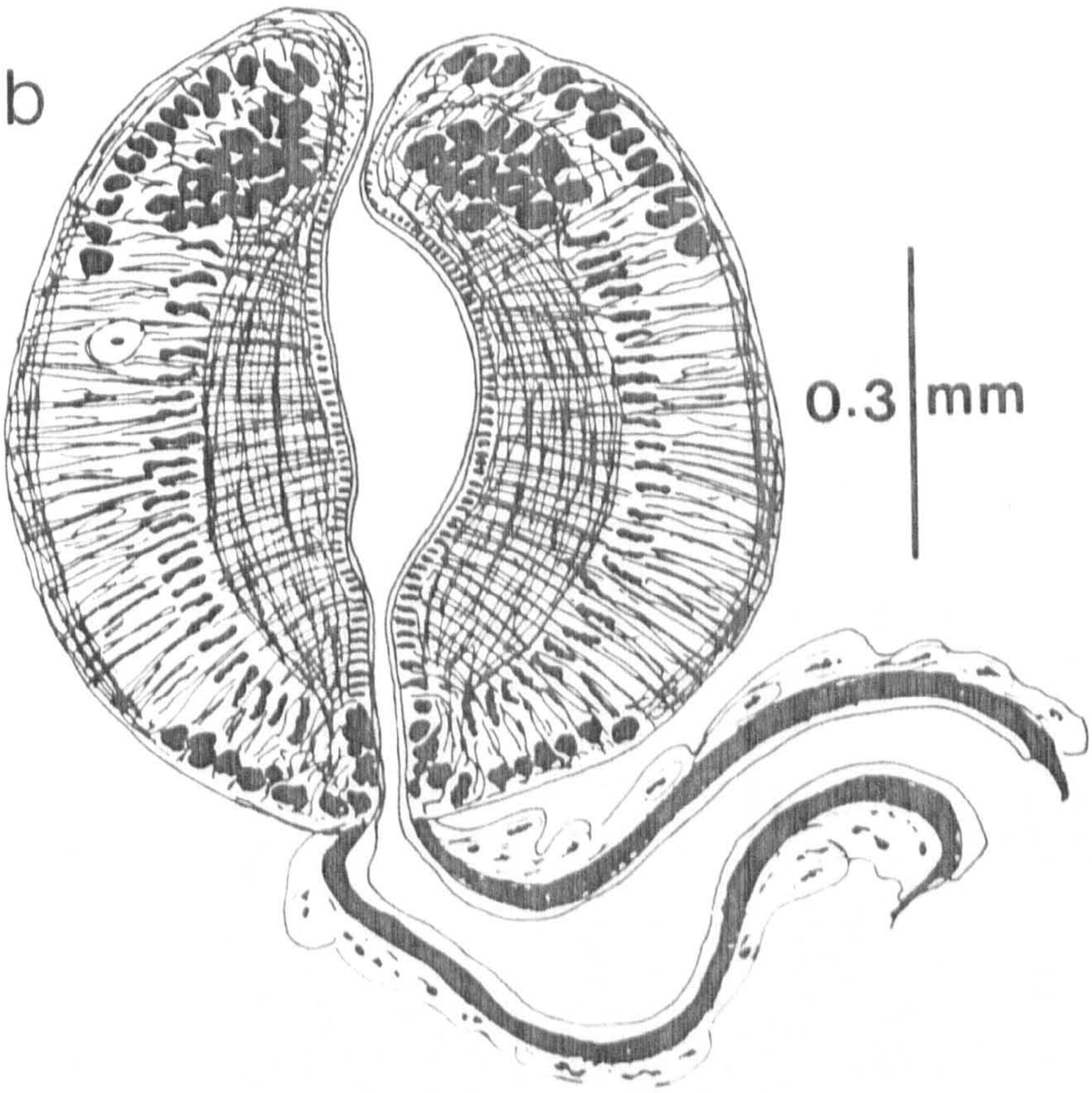
b. Pharynx (explanatum type) and oesophagus

a



1 mm

b



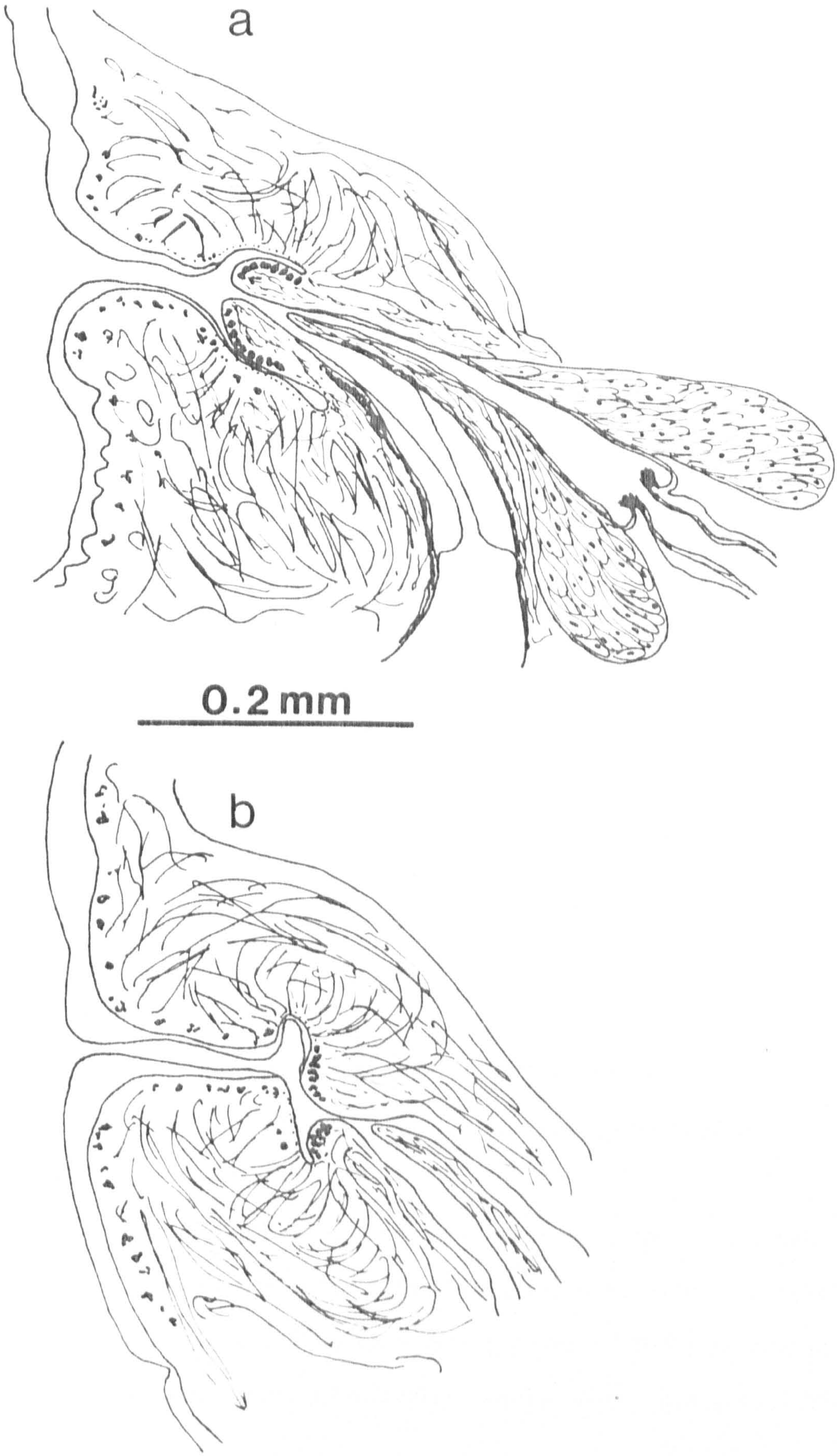
0.3 mm

FIGURE 119

Explanatum explanatum (Creplin, 1847) Fukui, 1929

(median sagittal section)

a - b. Terminal genitalium (explanatum type)



0.2 mm

Explanatum bathycotyle (Fischoeder, 1901) Yamaguti, 1958

TYPE SPECIMENS: United States National Parasite Collection, USDA, Beltsville, Maryland (USNMH Coll. No. 3372, co-type), from Bos kerabau in Ceylon (now Sri Lanka).

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collection

Bos indicus	Rangoon, Burma	British Museum (Natural History) coll. no. 1957. 12.266-280.
Bos taurus	Philippines	Author's own collection
Bubalus bubalis	Kuwait but host was imported from India	Prof. G. S. Nelson
	Philippines	Author's own collection
	Saigon, Vietnam and Sri Lanka	Naturhistoriska risksmuseet (Stockholm), Näsmark's material.
Goat	Malaysia	British Museum (Natural History) coll. no. 1962. 11.7.1001.

HABITAT: Liver, gall bladder and bile ducts

DESCRIPTION:

Body large, tapers anteriorly, broad and rounded posteriorly, slightly curved ventrally, 9.55-15.20 mm long, 3.54-4.38 mm in the dorso-ventral direction.

Acetabulum subterminal, enormous, 2.96-4.64 mm in external diameter in the dorso-ventral direction; ratio to body length 1:2.9 to 1:3.5; of the explanatum type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 8-16;

d.e.c.2, 25-38; d.i.c., 30-41; v.e.c., 10-15; v.i.c., 32-47; m.e.c., 8-15.

Pharynx 0.70-0.96 mm long, 0.55-0.88 mm in the dorso-ventral direction; ratio to body length 1:5.2 to 1:7.8, to the diameter of the acetabulum 1:3.5 to 1:3.9; of the explanatum type (sensu Näsmark, 1937) in median sagittal section; internal surface smooth, devoid of papillae. Oesophagus 0.48-1.56 mm long, nearly straight; musculature of wall relatively thin and uniform in thickness throughout its length, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, nearly straight in their course, terminate posteriorly anterior to the acetabulum.

Testes slightly lobed, directly tandem in middle third of the body; anterior testis 0.95-1.51 mm long, 1.46-1.83 mm in the dorso-ventral direction; posterior testis 0.96-1.57 mm long, 1.55-1.98 mm in the dorso-ventral direction; seminal vesicle long, thin-walled and strongly coiled; pars musculosa short and weakly developed; pars prostatica relatively small, 0.12-0.14 mm long and 0.12-0.18 mm wide.

Ovary subspherical, 0.45-0.65 by 0.46-0.65 mm, posterior to testes and anterior to acetabulum; Mehlis' gland close to ovary, 0.32-0.43 by 0.35-0.45 mm; Laurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface about 0.54-0.71 mm posteriorly to the excretory pore; uterus winds forward dorsal to the testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of oesophageal bifurcation to anterior border of acetabulum; egg 114-127 by 74-78 µm.

Genital pore opens on the ventral surface at level of the oesophageal bifurcation; terminal genitalium of the gracile type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to ovary and Mehlis' gland and antero-dorsal to acetabulum; excretory pore opens on the dorsal surface anteriorly to the Laurer's canal opening.

FIGURE 120

Explanatum bathycotyle (Fischoeder, 1901) Yamaguti, 1958

a. Whole worm, ventral view

b. Whole worm, sagittal view

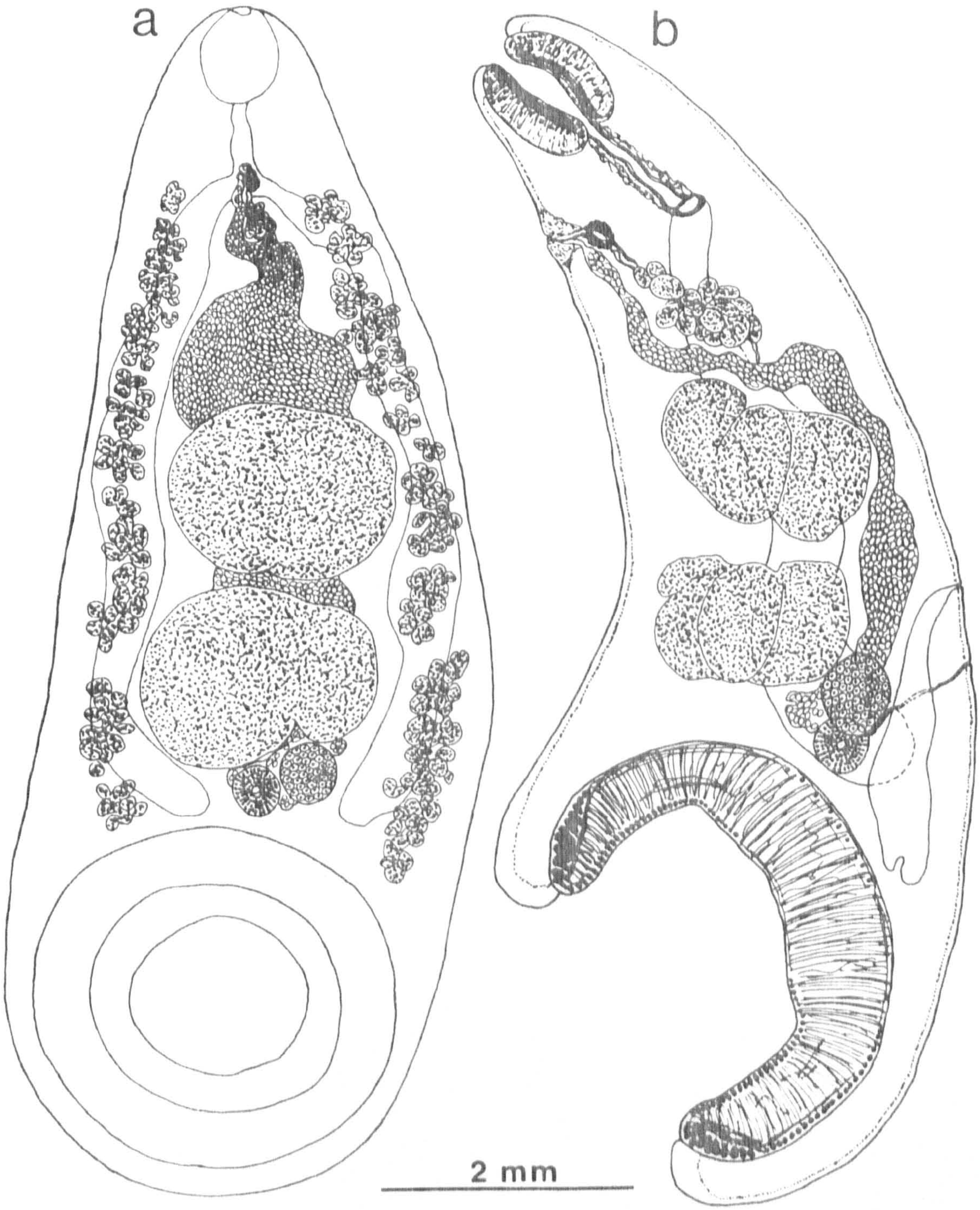

a
b
2 mm

FIGURE 121

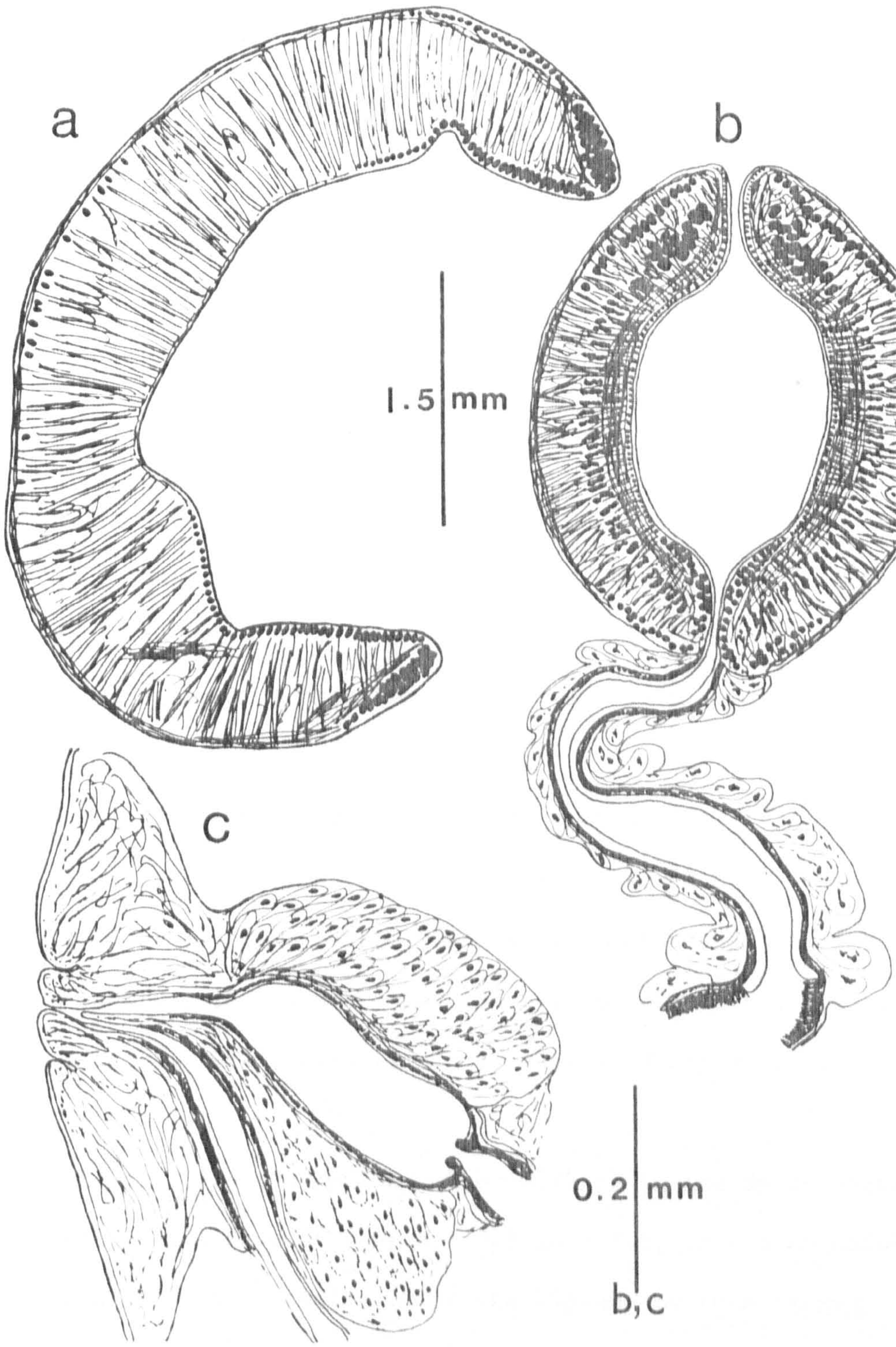
Explanatum bathycotyle (Fischoeder, 1901) Yamaguti, 1958

(median sagittal section)

a. Acetabulum (explanatum type)

b. Pharynx (explanatum type) and oesophagus

c. Terminal genitalium (gracile type) and pars prostatica


a
b
1.5 mm
C
0.2 mm
b, c

Explanatum anisocotylea (Faust, 1920) Yamaguti, 1958

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collection

Bubalus bubalis	India	London School of Hygiene & Tropical Medicine coll. no. 4432, labeled "Gastrothylax explanatum".
Goat	Taiping, Malaysia	British Museum (Natural History) coll. no. 1962. 11.7.1276-1280, labeled "G. siamense".

HABITAT: Liver and bile ducts

DESCRIPTION:

Body small, tapers anteriorly, broad and rounded posteriorly, curved ventrally, 4.88-6.30 mm long, 3.30-4.10 mm in the dorso-ventral direction. Acetabulum and pharynx very close to each other.

Acetabulum subterminal, enormous, 3.00-3.48 mm in external diameter in the dorso-ventral direction; ratio to body length 1:1.4 to 1:2.3; of the explanatum type in median sagittal section (sensu Näsmark, 1937); number of circular muscle units, d.e.c.1, 8-14; d.e.c.2, 20-29; d.i.c., 27-31; v.e.c., 9-15; v.i.c., 30-41; m.e.c.3-8.

Pharynx 0.70-0.99 mm long, 0.60-0.88 mm in the dorso-ventral direction; ratio to body length 1:5.3 to 1:7.5, to the diameter of the acetabulum 1:3.7 to 1:4.5; of the explanatum type (sensu Näsmark, 1937) in median sagittal section; internal surface smooth, devoid of papillae. Oesophagus 0.48-0.56 mm long, musculature of wall relatively thin and uniform in thickness throughout its

length, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral fields of the body, form dorso-ventral bends during their course, blind ends at level of and dorsal to acetabulum and directed medially.

Testes slighltly lobed, obliquely tandem in middle third of the body; anterior testis 0.51-1.03 mm long, 1.03-1.34 mm in the dorso-ventral direction; posterior testis dorsal to acetabulum, 0.56-0.85 mm long, 1.02-1.49 mm in the dorso-ventral direction. Seminal vesicle relatively long, thick-walled and coiled; pars musculosa short, straight and weakly developed; pars prostatica small, 0.22-0.25 mm long and 0.16-0.18 mm wide.

Ovary subspherical, 0.43-0.56 by 0.45-0.50 mm, dorsal to acetabulum and posterior to thestes; Mehlis' gland close to ovary, 0.35-0.37 by 0.25-0.37 mm; Laurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface posteriorly to the excretory pore; uterus winds forward dorsal to the testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of pharynx to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 135-160 by 70-85 µm.

Genital pore opens on the ventral surface at level of the pharynx; terminal genitalium of the explanatum type (sensu Näsmark, 1937) in median sagittal section but with weakly developed genital sphincter.

Excretory vesicle dorsal to acetabulum, ovary, Mehlis' gland and posterior testis; excretory pore opens on the dorsal surface at level of the posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 122

Explanatum anisocotylea (Faust, 1920) Yamaguti, 1958

a. Whole worm, ventral view

b. Whole worm, sagittal view

c. Pharynx (explanatum type) and oesophagus, median sagittal section

d. Terminal genitalium (explanatum type) and pars prostatica, median sagittal section

a

b

1 mm

c

0.5 mm

d

0.2mm

DISCUSSION

Näsmark (1937) listed for his genus Gigantocotyle the same species that Fukui (1929) has previously listed for his subgenus Explanatum. According to the International Code for Zoological Nomenclature, subgenera have the same nomenclatural status as genera. Consequently, Explanatum should have priority as it supercedes Gigantocotyle. However, by tautonomy and previous designation by the original authors, the type species for each genus is different, gigantocotyle (Brandes in Otto, 1896) for the former and explanatum (Creplin, 1847) for the latter. Morphologically, the two species differ from each other in one important generic character, i.e. the development of the pars musculosa; that of gigantocotyle is long, well developed and convoluted while that of explanatum is short, weakly developed and almost straight. The rest of the species assigned to both taxa can also be divided into two groups based on this character. In view of the importance attached to the above character as already explained earlier in this work, the genus Gigantocotyle Näsmark, 1937 is here upheld but restricted to include only those species with enormous acetabulum and long, well developed and convoluted pars musculosa and the subgenus Explanatum Fukui, 1929 is raised to full generic rank to contain only those species with enormous acetabulum and short, weakly developed and almost straight pars musculosa. Accordingly, the species arrangement for each genus is as follows: Gigantocotyle Näsmark, 1937 = G. gigantocotyle (Brandes in Otto, 1896) Näsmark, 1937 (type species); G. formosanum (Fukui, 1929) Näsmark, 1937; G. symmeri Näsmark, 1937; G. duplicitestorum Näsmark, 1937 and

G. lerouxi Yeh, 1957. Explanatum (Fukui, 1929) status emended = E. explanatum (Creplin, 1847) Fukui, 1929 (type species); E. bathycotyle (Fischoeder, 1901) Yamaguti, 1958; E. anisocotylea (Faust, 1920) Yamaguti, 1958; E. fraternum (Stiles and Goldberger, 1910) Yamaguti, 1958 and E. siamense (Stiles and Goldberger, 1910) Yamaguti, 1958. However, three of the above species as will be explained later are junior synonyms. Because of the enormous acetabulum, both genera can be easily separated from the rest of the genera in the family Paramphistomidae. For this reason, the writer does not accept the synonymy of Gigantocotyle with Paramphistomum nor the retention of Explanatum just as a subgenus under Paramphistomum as proposed by Yamaguti (1958, 1971).

Yeh (1957) described Gigantocotyle lerouxi from the stomach of the red lechwe (Kobus leche) in Northern Rhodesia (now Zambia). It was separated from G. formosanum by being larger and in having a different geographical distribution. It was not however differentiated from the very closely related species, G. symmeri or from the rest of the species in the genus. The type specimens as indicated were deposited in the London School of Hygiene and Tropical Medicine Helminth Collection but these could not be found in the said collection. In Dinnik's collection of amphistomes housed in the Commonwealth Institute of Helminthology are sections of several specimens labeled "G. lerouxi, co-types". This material came from the same batch of specimens from which Yeh made his sections and subsequently based his description of the species. Re-examination of the said material showed that the specimens are identical with the types of G. symmeri Näsmark, 1937 loaned from

the Naturhistoriska riksmuseet, Stockholm. The explanatum type of terminal genitalium to which Yeh referred his species is erroneus. It is infact of the gigantocotyle type (sensu Näsmark, 1937) because it is very prominent, has a large and well developed genital papilla and has both genital sphincter and sphincter papilla. Besides, Yeh's own figure (Fig. 1) clearly shows that the terminal genitalium is of the gigantocotyle type. Examination of several materials from the same host and locality revealed specimens belonging to the genus identifiable only as G. symmeri. Gigantocotyle lerouxi Yeh, 1957 therefore is regarded here as a junior synonym of G. symmeri Näsmark, 1937.

Näsmark (1937) referred the acetabulum of G. gigantocotyle to the explanatum type but specimens of this species examined in this work revealed that the acetabulum is not of that type. In the ventral exterior circular series of the acetabulum in this species is a second group of small circular muscle units numbering from 7-12, very close to the external wall and separated from the larger group of circular muscle units by a band of oblique muscle fibres. Because of the small size of the units and their proximity to the external wall, Näsmark probably failed to observed them. The presence of a second group of circular muscle units in the ventral exterior series is lacking in all types of acetabulum so far known. In view of this, the acetabulum of G. gigantocotyle is designated here as the gigantocotyle type (new type).

There are some important taxonomic characters that need mentioning here which were not included in previous descriptions of G. gigantocotyle and G. symmeri. These are: the character of

the vitellaria which are confluent dorso-medially both in their anterior and posterior limits in both species and the lining of the lumen of the oesophagus of G. symmeri which consists of two kinds, hyaline layer on the anterior part and ciliated epithelium on the posterior part.

The species Paramphistomum birmense Railliet, 1924 which was moved by Näsmark (1937) to the genus Gigantocotyle is regarded here species inquirenda for reasons already discussed under the genus Paramphistomum.

Only four species are considered valid under the genus Gigantocotyle namely: G. gigantocotyle (Brandes in Otto, 1896) Näsmark, 1937; G. formosanum (Fukui, 1929) Näsmark, 1937; G. symmeri Näsmark, 1937 and G. duplicitestorum Näsmark, 1937. A key to separate the above species is given at the end of this discussion.

Explanatum fraternum and E. siamense were originally described by Stiles and Goldberger (1910) under the genus Paramphistomum. The former consisted of only two specimens which were in very poor condition. and was differentiated from P. explanatum (now Explanatum explanatum) only by slight differences in the relative positions of the various organs. The latter was also differentiated from the former as above. Re-examination of the type specimens of both species loaned from the United States National Parasite Collection, USDA, Beltsville, Maryland (USNMH 366 - P. fraternum, USNMH 997 - P. siamense) revealed that both species are identical with Explanatum explanatum. The slight differences in the relative positions of the various organs may be attributed to the contraction

of their specimens as these were poorly preserved. Consequently, Paramphistomum fraternum Stiles and Goldberger, 1910 and P. siamense Stiles and Goldberger, 1910 are regarded here as synonyms of Explanatum explanatum (Creplin, 1847) Fukui, 1929.

Since Fischoeder (1901, 1902, 1903) described Paramphistomum bathycotyle, several subsequent authors have doubted its validity. Maplestone (1923) synonymized it with P. cervi, a view followed by Sprehn (1932), Fukui (1929), Stunkard (1929), Travassos (1934), and Dawes (1936, 1956). Stiles and Goldberger (1910), Gedoelst (1911), Railliet (1924) and Gupta (1951) maintained it as a separate species under the genus Paramphistomum. Näsmark (1937) accepted its validity and moved it to the genus Gigantocotyle, a view shared by Willmott (1950a) and Jain (1978). Kulasire and Seneviratne (1956) and Singh (1958) considered it a synonym of Gigantocotyle explanatum. Yamaguti (1958, 1971) listed it as a separate species under the subgenus Explanatum of the genus Paramphistomum. This study has shown that the species in question is valid and should be assigned to the genus Explanatum where it can be differentiated from the other species of the genus. Contrary to Näsmark's reference of its terminal genitalium to the explanatum type, this study has shown after re-examination of the co-type loaned from the United States National Parasite Collection, USDA, Beltsville, Maryland (USNMH Coll. No. 3372) that the terminal genitalium is not of that type but of the gracile type (sensu Näsmark, 1937).

Only three species of the genus Explanatum are considered valid namely: Explanatum explanatum (Creplin, 1847) Fukui, 1929; E. bathycotyle (Fischoeder, 1901) Yamaguti, 1958 and E. anisocotylea

(Faust, 1920) Yamaguti, 1958 and they are separable by a key given below.

Key to the species of the genus Gigantocotyle Näsmark, 1937

1. Vitellaria confluent dorso-medially in their anterior and posterior limits; terminal genitalium of the gigantocotyle type - 2

   Vitellaria not confluent dorso-medially; terminal genitalium of the microbothrium type - - - - - - - - - - 3

2. Acetabulum of the symmeri type; posterior part of oesophagus lined by ciliated epithelium; parasite of ruminants - - - - - - - - - - - - - - - G. symmeri

   Acetabulum of the gigantocotyle type; posterior part of oesophagus not lined by ciliated epithelium; parasite of the hippopotamus - - - - - - - G. gigantocotyle

3. Acetabulum of the duplicitestorum type; parasite of the hippopotamus - - - - - - - - - - - - - G. duplicitestorum

   Acetabulum of the symmeri type; parasite of ruminants - G. formosanum

Key to the species of the genus Explanatum (Fukui, 1939) status emended

1. Terminal genitalium of the explanatum type - - - - - - - - - - 2

   Terminal genitalium of the gracile type - - - - E. bathycotyle

2. Pharynx and acetabulum very close together; body small; caeca wavy - E. anisocotylea

   Pharynx and acetabulum far apart; body large; caeca almost straight - - - - - - - - - - - - - - - - - E. explanatum

Revision of the genus Cotylophoron Stiles and Goldberger, 1910

INTRODUCTION

Stiles and Goldberger (1910) established the genus Cotylophoron for Paramphistomum cotylophorum Fischoeder, 1901 on the basis of the presence of a genital sucker. At the same time, they described Cotylophoron indicum as a new species from Ovis aries in India.

With the exception of Fukui (1929) who reduced the genus to subgeneric status and Dawes (1936) who entirely rejected it, subsequent authors including Gedoelst (1911), Maplestone (1923), Railliet (1924), Stunkard (1929), Travassos (1934), Näsmark (1927), Skrjabin (1949), Baer and Joyeux (1961), Yamaguti (1958, 1971), Mukherjee and Chauhan (1965) and Lee and Lowe (1971) accepted the genus. Maplestone (1923) moved Paramphistomum minutum Leiper, 1910 and P. sellsi Leiper, 1910, both parasites of the hippopotamus, to the genus but regarded both as one and the same species, the former species has priority over the latter. He also regarded Cotylophoron indicum as a synonym of C. cotylophorum. Travassos (1934), without examining materials of the above three species, accepted Maplestone's transfer of Leiper's species but regarded each as distinct and valid and also followed Maplestone's synonymy of C. indicum. Näsmark (1937) examined species of Paramphistomum minutum and P. sellsi and came to the conclusion that each is distinct and valid but transfered both to his genus Nilocotyle in new combinations.

Harshey (1934) added to the genus three new species namely: Cotylophoron ovatum, C. orientalis and C. elongatum all from sheep and goats in India. Leiper (1935) described briefly and without illustration C. okapi from an okapi that died in the London Zoo. From the same host, Baer (1936) described C. congolense but later (1950) synonymized it with C. okapi.

Näsmark (1937) revised the genus to include Cotylophoron cotylophorum and C. indicum and two other new species, C. jacksoni and C. fuelleborni from Alcelaphus cokei and various ruminants in Africa. He accepted the validity of C. indicum without examining the type specimens and redescribed it on the basis of materials from cattle in the Sudan. Although he was aware of C. congolense Baer, 1936, as he listed the paper under adendum, no comment on its status was given. He was unaware though of Harshey's (1934) and Leiper's (1935) species as these were not included in his bibliography or in the adendum.

Price and McIntosh (1953) described Cotylophoron panamensis and C. noveboracensis from Ovis aries in Panama and the U.S.A. respectively. They removed C. okapi and Harshey's three species (1934) from the genus because Laurer's canal does not cross the excretory vesicle in these species and tentatively assigned them under the genus Orthocoelium (Stiles and Goldberger, 1910). They re-examined the type specimens of C. indicum Stiles and Goldberger, 1910 and came to the conclusion that the species belongs to the genus Paramphistomum, for which they gave the new name P. thapari as P. indicum is pre-occupied.

From the U.S.S.R., two species were added to the genus namely: Cotylophoron skrjabini Mitskevich (1958) from Rangifer tarandus and C. vigisi Davydova, 1963 from long-horned cattle in the Primorsk Region. The latter species however was reported by the same author under her married name (Davydova-Velichko, 1964) after a careful examination of the type specimens and new materials that it is in fact Paramphistomum ichikawai Fukui, 1922. From sheep in India, C. madrasense Gupta, 1958 and C. chauhani Gupta and Gupta, 1972 were described as new species under the genus. Mukherjee (1963) unaware of C. skrjabini Mitskevich, 1958 described specimens from Capra hircus in India as C. skrjabini new species. Since the name is pre-occupied, Mukherjee and Chauhan (1965) gave the name, C. bareilliense for it. They also regarded C. orientalis Harshey, 1934 and C. ovatum Harshey, 1934 as synonyms of C. indicum Stiles and Goldberger, 1910 and Ceylonocotyle scoliocoelium (Fischoeder, 1901) (now Orthocoelium scoliocoelium) respectively.

New species have been described recently under the genus. These are: Cotylophoron ottoi Gupta and Bakhshi in Gupta and Nakhasi, 1977 from Bos indicus and Bubalus bubalis in India; C. macrosphinctris Sey and Graber, 1979 from Syncerus caffer in the Central African Empire and C. xiangjiangense Wang, 1979 from Bubalus bubalis and C. guangdongense Wang, 1979 from Bubalus bubalis and Bos taurus in China.

The writer in a published paper (1980c) which forms part of this thesis has shown after re-examination of the type specimens C. okapi Leiper, 1935 and C. congolense Baer, 1936 are distinct and separate species. Both species cannot be retained under the genus

Cotylophoron because of the Laurer's canal which does not cross the excretory vesicle or duct nor they can be assigned to the genus Orthocoelium as proposed by Price and McIntosh (1953) nor to any of the remaining genera in the subfamily Orthocoeliinae because of the presence of a genital sucker and the well developed pars musculosa. The genus Leiperocotyle was therefore erected under the subfamily Orthocoeliinae for their reception. For the same reasons, C. elongatum Harshey, 1934 and C. orientalis Harshey, 1934 were assigned tentatively to the new genus pending re-examination of the type specimens.

This revision deals with species described under Cotylophoron with Laurer's canal crossing the excretory vesicle or duct. After examination of new materials and re-examination of available type specimens, this study has shown that of the 15 species with this character, only seven species are valid. They are here redescribed and illustrated and their synonymies discussed.

GENERIC DIAGNOSIS

Body conical, almost straight or may bend ventrally. Acetabulum subterminal, small to moderate in size. Ventral pouch absent. Genital sucker present, with or without genital sphincter. Pharyngeal pouch or diverticle absent; oesophagus with or without bulb or posterior sphincter; caeca in lateral sides of the body, form dorso-ventral bends, blind ends directed dorsally. Testes lobed, directly or obliquely tandem, juxtaposed or obliquely horizontal; seminal vesicle thin-walled and deeply coiled; pars musculosa well developed and convoluted; pars prostatica small and weakly developed. Ovary and Mehlis' gland posterior to the testes; uterus winds forward, dorsal to the testes then ventral to the male ducts; Laurer's canal crosses the excretory vesicle or duct; vitellaria in lateral fields, may or may not be confluent dorso-medially in their anterior or posterior limits. Parasitic in the stomach of ruminants.

Type species: Cotylophoron cotylophorum (Fischoeder, 1901)
Stiles and Goldberger, 1910

Cotylophoron cotylophorum (Fischoeder, 1901) Stiles and Goldberger, 1910

Synonym: Cotylophoron guangdongense Wang, 1979

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos indicus	Musoma and Tarime, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection
	Mwanza Abattoir, Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Cattle	Nakuru, Kenya	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Uganda	London School of Hygiene & Tropical Medicine

HABITAT: Rumen and reticulum

DESCRIPTION:

Body conical, 4.82-8.93 mm long, 2.14-3.45 mm in the dorso-ventral direction. Body surface has papillae around oral opening, on the rim of the genital sucker and around the acetabular opening. Those on the latter are much more smaller and randomly arranged than those on the first two.

Acetabulum subterminal, 1.51-2.34 mm in external diameter in the dorso-ventral direction; ratio to body length 1:2.5 to 1:4.3; of the cotylophoron type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 10-16; d.i.c., 36-48; v.e.c., 9-14; v.i.c., 45-59; m.e.c., 10-14.

Pharynx 0.61-1.01 mm long, 0.60-0.85 mm in the dorso-ventral direction; ratio to body length 1:7.3 to 1:10, to the diameter of the acetabulum 1:2 to 1:2.3; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section; internal surface lined by small dome-shaped papillae. Oesophagus 0.37-1.01 mm long, with a strong muscular posterior bulb about 0.45-0.55 mm in diameter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form about six dorso-ventral bends, reach level of acetabulum with the blind ends directed dorsally.

Testes deeply lobed, directly or obliquely tandem in middle third of the body; anterior testis 0.61-1.05 mm long, 1.20-2.02 mm in the dorso-ventral direction; posterior testis 0.73-1.98 mm long, 2.10-2.63 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa, thick-walled, well developed and convoluted; pars prostatica small and weakly developed.

Ovary subspherical, 0.30-0.49 by 0.49-0.55 mm, posterior to testes; Mehlis' gland close to ovary, 0.23-0.28 by 0.25-0.27 mm; Laurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface about 0.35-0.56 mm posteriorly to the excretory pore; uterus winds forward, dorsal to the testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of pharynx to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 125-141 by 55-65 µm.

Genital pore opens on the ventral surface at a level posterior to the oesophageal bifurcation; terminal genitalium of the cotylophoron type (sensu Näsmark, 1937) in median sagittal section

with the genital sucker measuring about 0.89-1.31 mm in diameter; genital sucker slightly larger or as larges as the pharynx, its ratio to the diameter of the acetabulum 1:2 to 1:2.2.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface anteriorly to the Laurer's canal opening.

FIGURE 123

Cotylophoron cotylophorum (Fischoeder, 1901)
Stiles and Goldberger, 1910
(SEM)

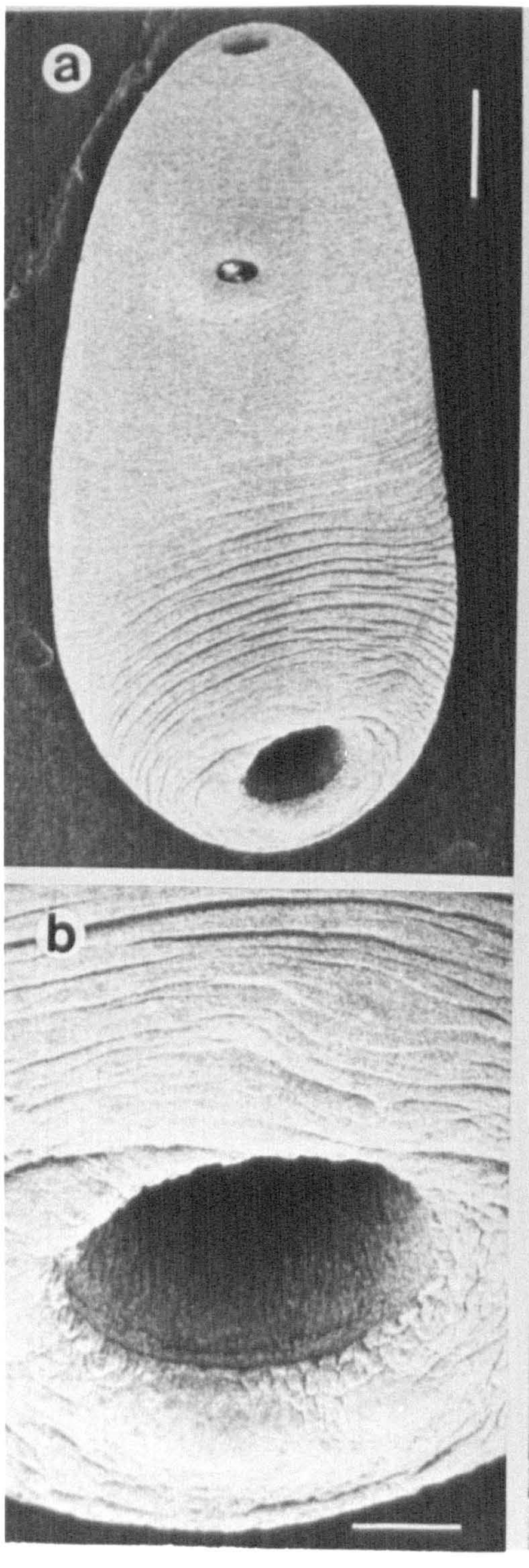
a. Whole worm, ventral view (scale bar = 300 µm)

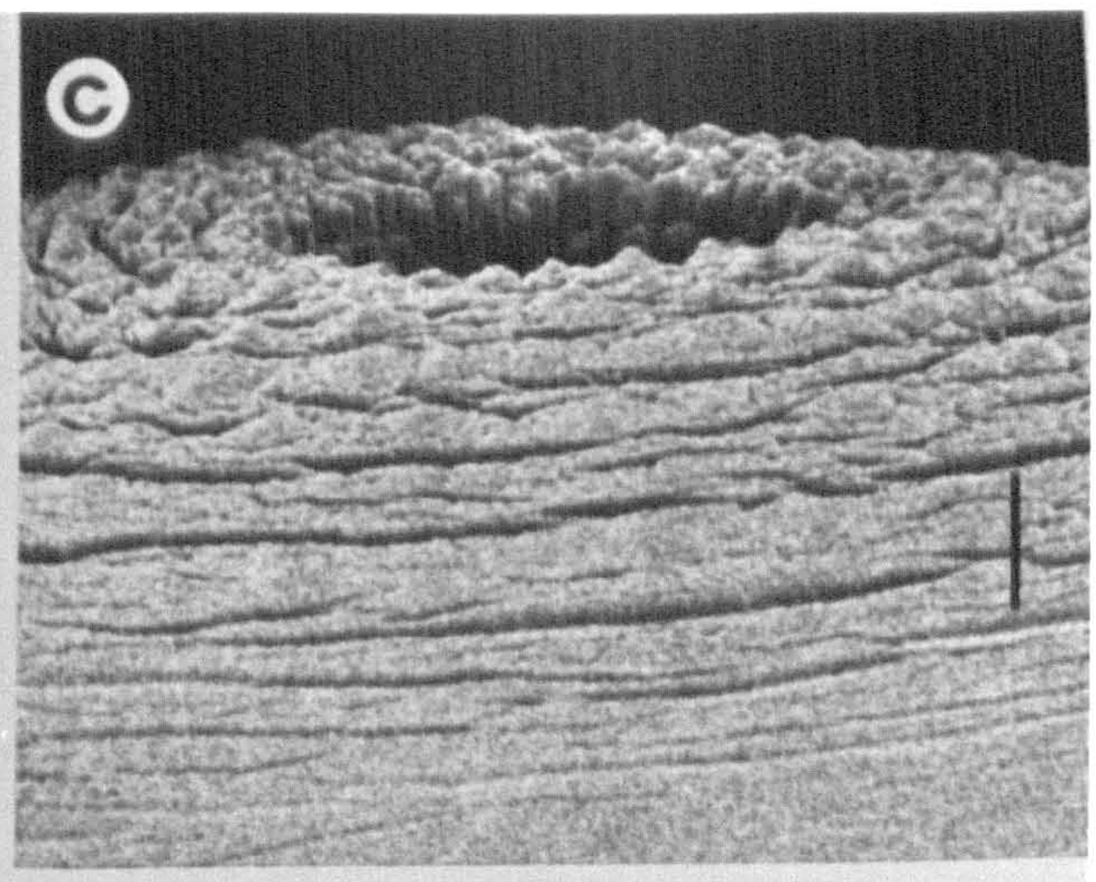
b. Acetabular region (scale bar = 100 µm)

c. Oral end, note papillae (scale bar = 300 µm)

c. Genital pore region, note papillae (scale bar = 50 µm)

d. Another genital pore region (scale bar = 50 µm)


a
b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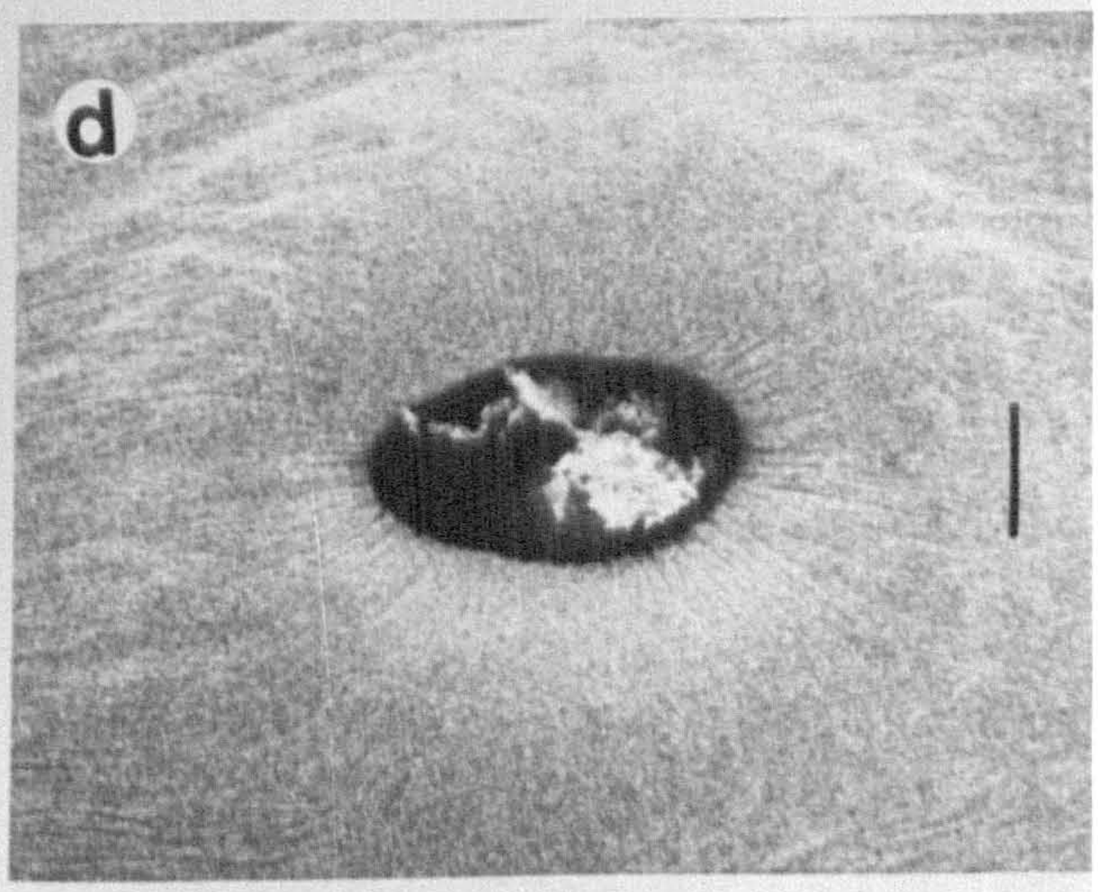
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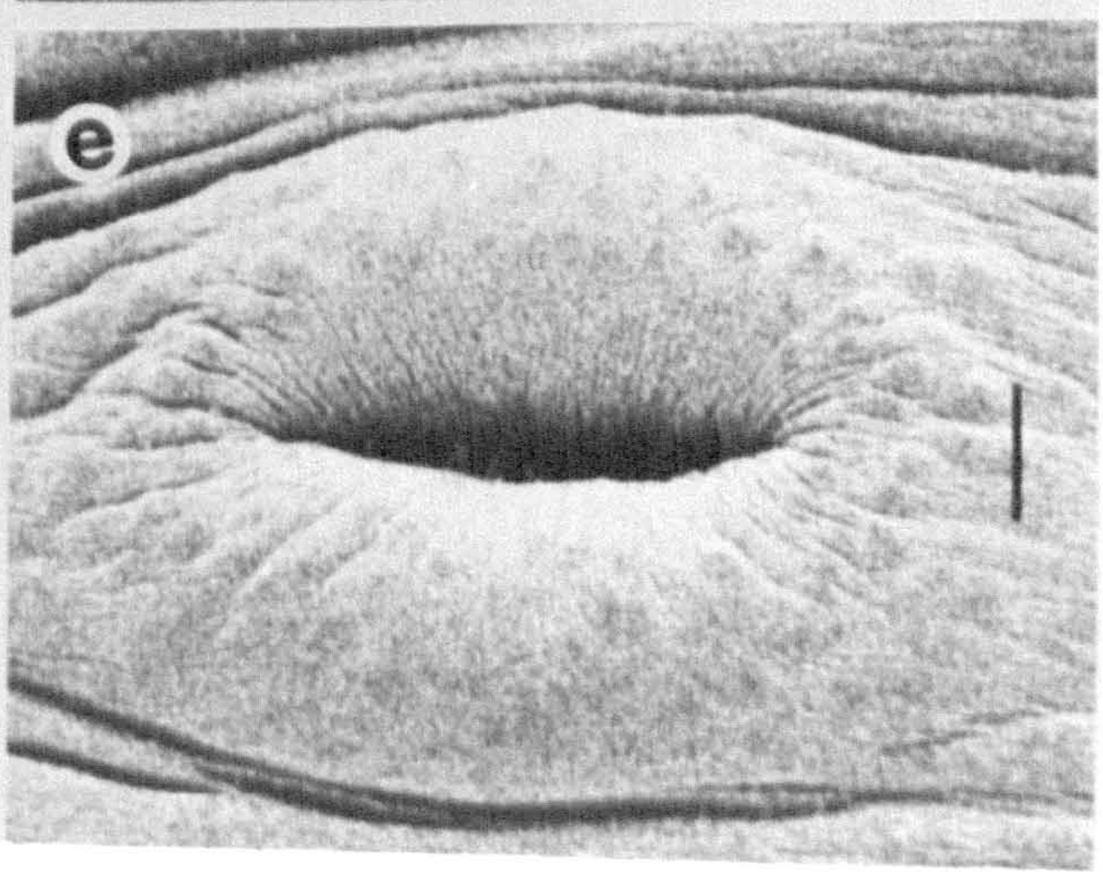
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FIGURE 124

Cotylophoron cotylophorum (Fischoeder, 1901)
Stiles and Goldberger, 1910

a. Whole worm, ventral view

b. Whole worm, sagittal view

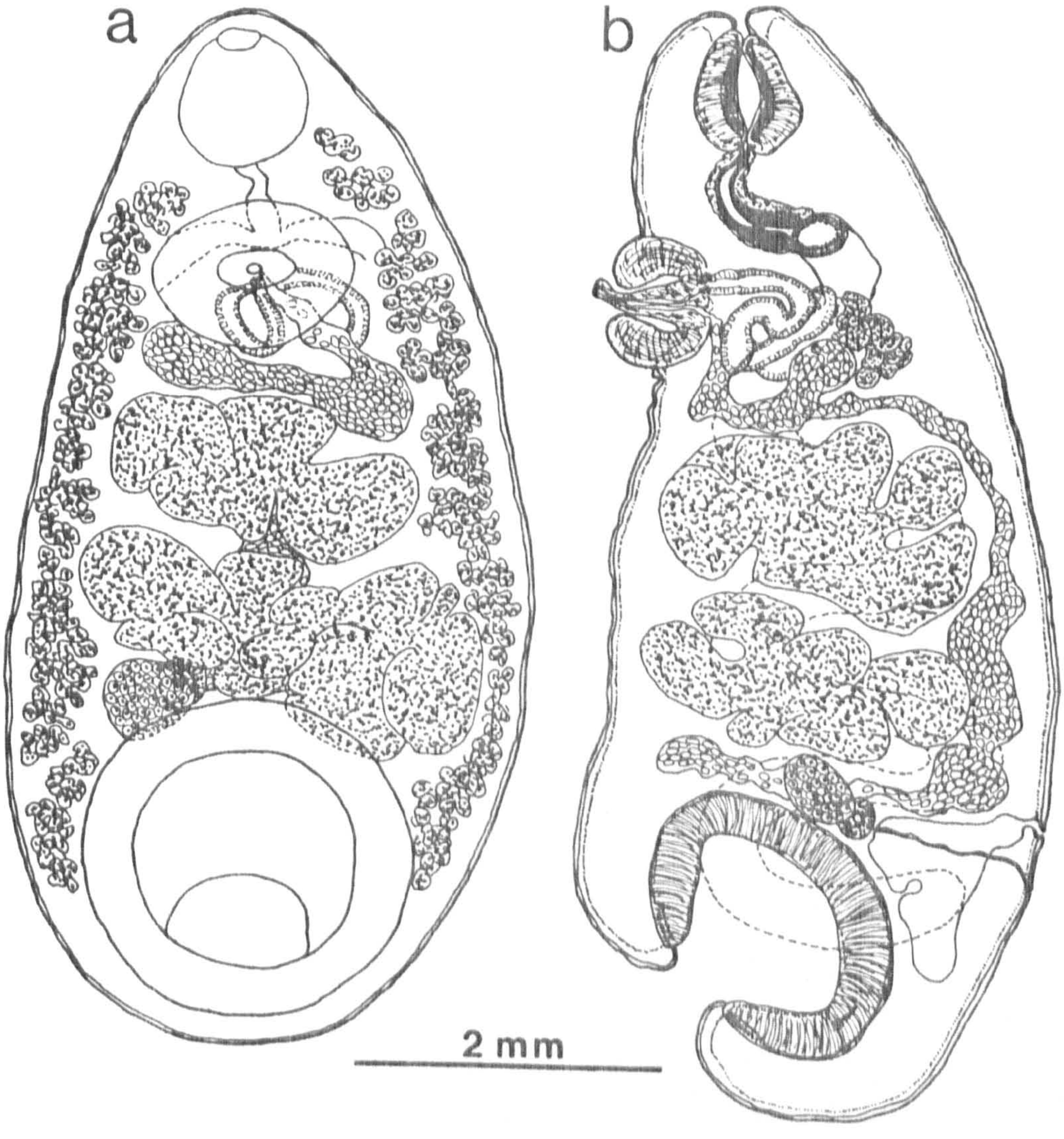

a
b
2 mm

FIGURE 125

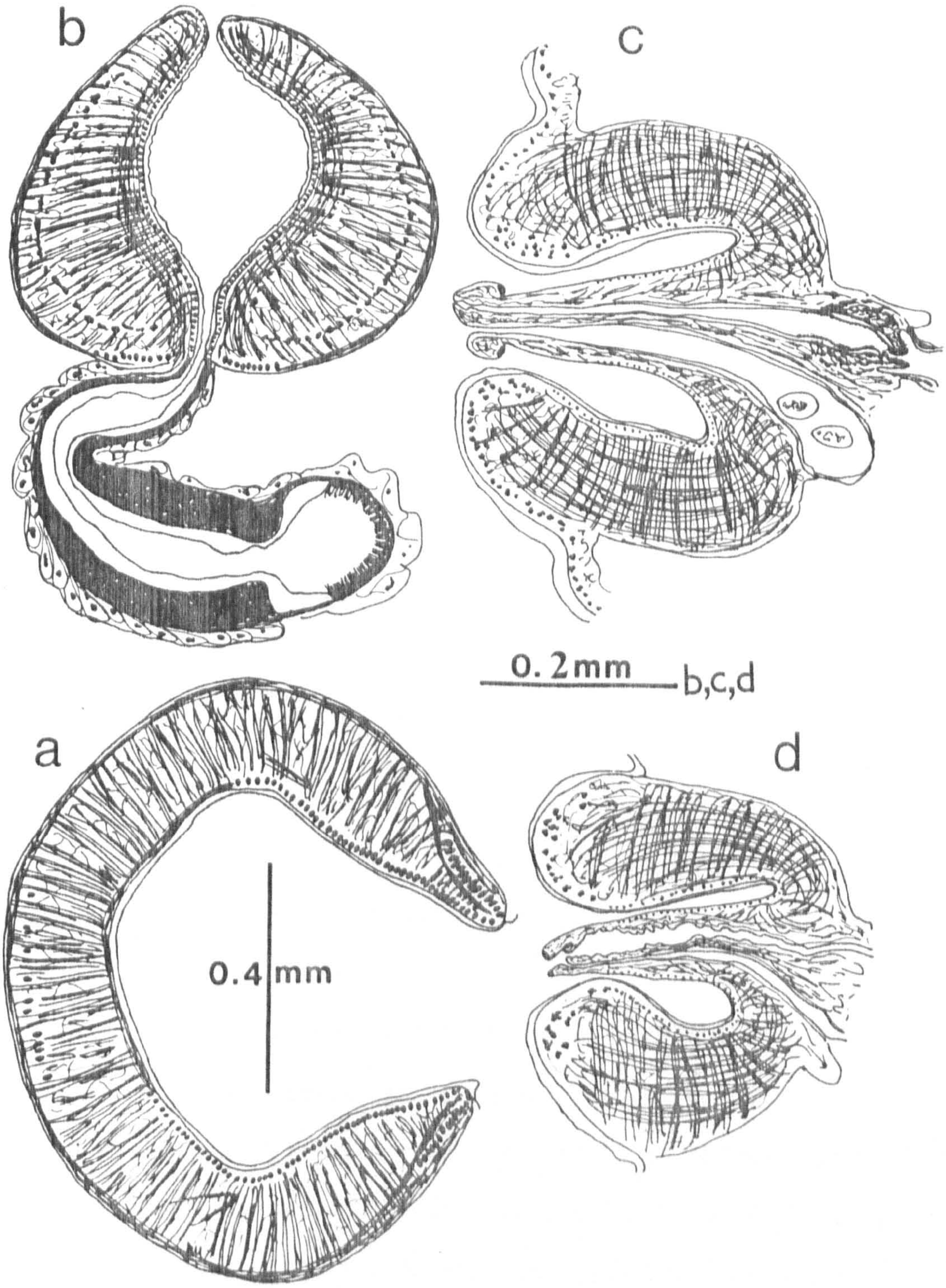
Cotylophoron cotylophorum (Fischoeder, 1901)
Stiles and Goldberger, 1910
(median sagittal section)

a. Acetabulum (cotylophoron type)

b. Pharynx (calicophoron type) and oesophagus, note muscular posterior bulb.

c. Terminal genitalium (cotylophoron type)

d. Another terminal genitalium (cotylophoron type)


b
c
0.2mm
b,c,d
a
0.4mm
d

Cotylophoron jacksoni Näsmark, 1937

TYPE SPECIMENS: Naturhistoriska riksmuseet, Stockholm (RMev. Sthlm. Coll. No. R341) from hartebeest (kongoni) and Alcelaphus cokei in Mount Elgon (now part of Kenya and part of Uganda), East Africa.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Alcelaphus buselaphus	Chinsali and Chunga, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L LeRoux collection.
Bos indicus	Mburara, Uganda	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Cattle	Gambia	London School of Hygiene & Tropical Medicine
Hippotragus niger	Tanzania	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.

HABITAT: Rumen

DESCRIPTION:

Body conical, more or less straight, 7.50-9.86 mm long, 2.45-3.32 mm in the dorso-ventral direction, usually tapers anteriorly.

Acetabulum subterminal, 1.42-2.30 mm in external diameter in the dorso-ventral direction; ratio to body length 1:4.6 to 1:5.6; of the cotylophoron type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 10-17; d.i.c., 36-48; v.e.c., 15-21; v.i.c., 35-46; m.e.c., 5-12.

Pharynx 0.85-1.09 mm long, 0.48-0.58 mm in the dorso-ventral direction; ratio to body length 1:8.5 to 1:9.3, to the diameter of the acetabulum 1:1.5 to 1:1.7; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section; internal surface lined by small dome-shaped papillae. Oesophagus 0.85-0.96 mm long, musculature of wall uniformly thick, no bulb or posterior sphincter, lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form about five dorso-ventral bends, reach anterior border of acetabulum with the blind ends directed dorsally.

Testes deeply lobed, directly tandem in posterior two third of the body; anterior testis 1.21-1.55 mm long, 1.55-1.96 mm in the dorso-ventral direction; posterior testis 0.99-1.32 mm long, 1.55-1.62 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa, thick-walled, well developed and convoluted; pars prostatica small and weakly developed.

Ovary subspherical, 0.48-0.63 by 0.53-0.65 mm, posterior to testes and on one side of the median line; Mehlis' gland close to ovary, 0.36-0.48 by 0.39-0.43 mm; Laurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface about 0.30-0.45 mm posteriorly to the excretory pore; vitellaria in lateral fields, extend from level of the oesophageal bifurcation to the anterior border of the acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 125-130 by 53-60 µm.

Genital pore opens on the ventral surface at a level posterior to the oesophageal bifurcation; terminal genitalium of the cotylophoron type (sensu Näsmark, 1937); genital sucker 0.86-1.19 mm in diameter, as large as the pharynx, ratio to the diameter of the acetabulum 1:1.5 to 1:1.8.

Excretory vesicle antero-dorsal to acetabulum, dorsal to ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level of the posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 126

Cotylophoron jacksoni Näsmark, 1937

a. Whole worm, ventral view

b. Whole worm, sagittal view

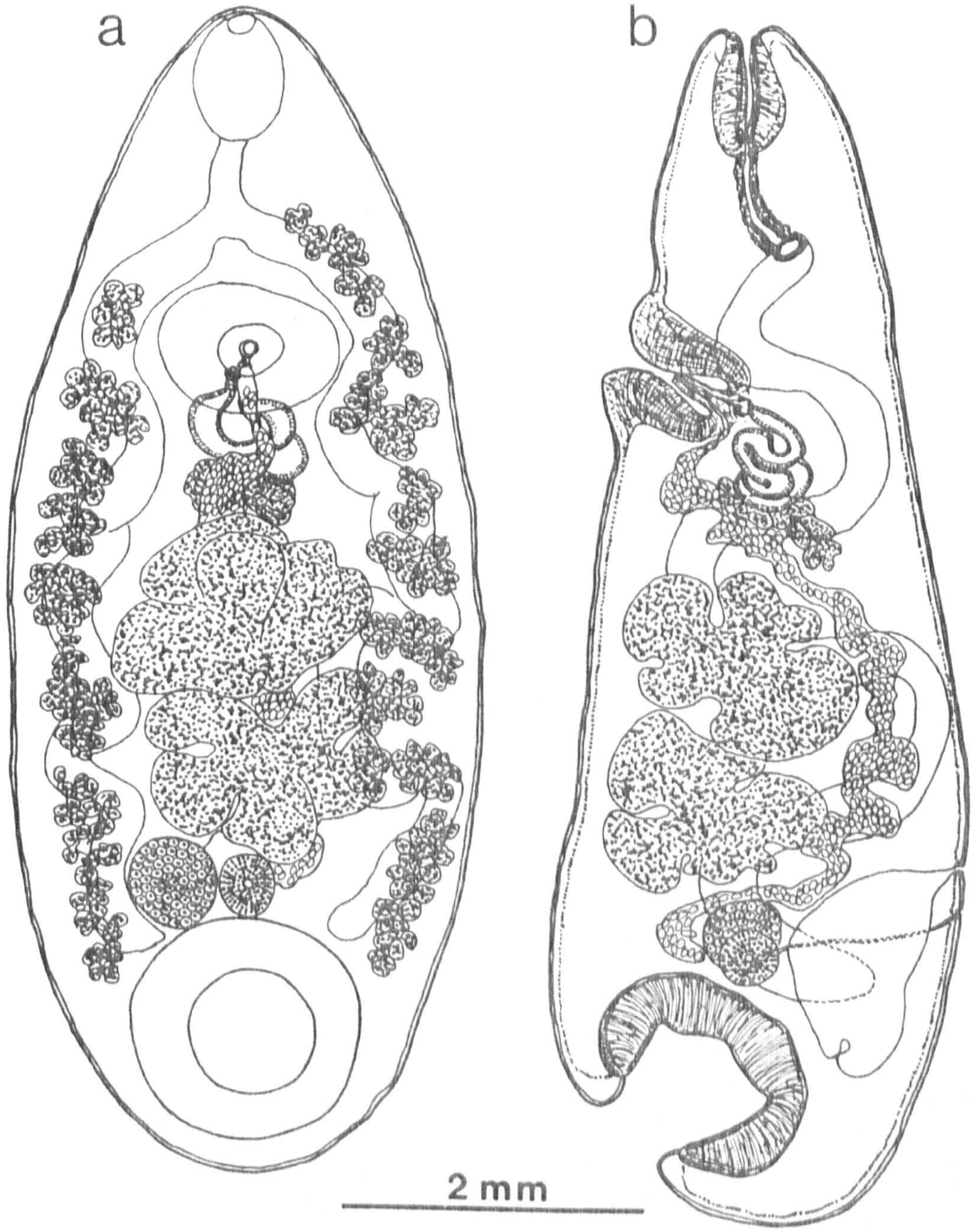

a
b
2 mm

FIGURE 127

Cotylophoron jacksoni Näsmark, 1937

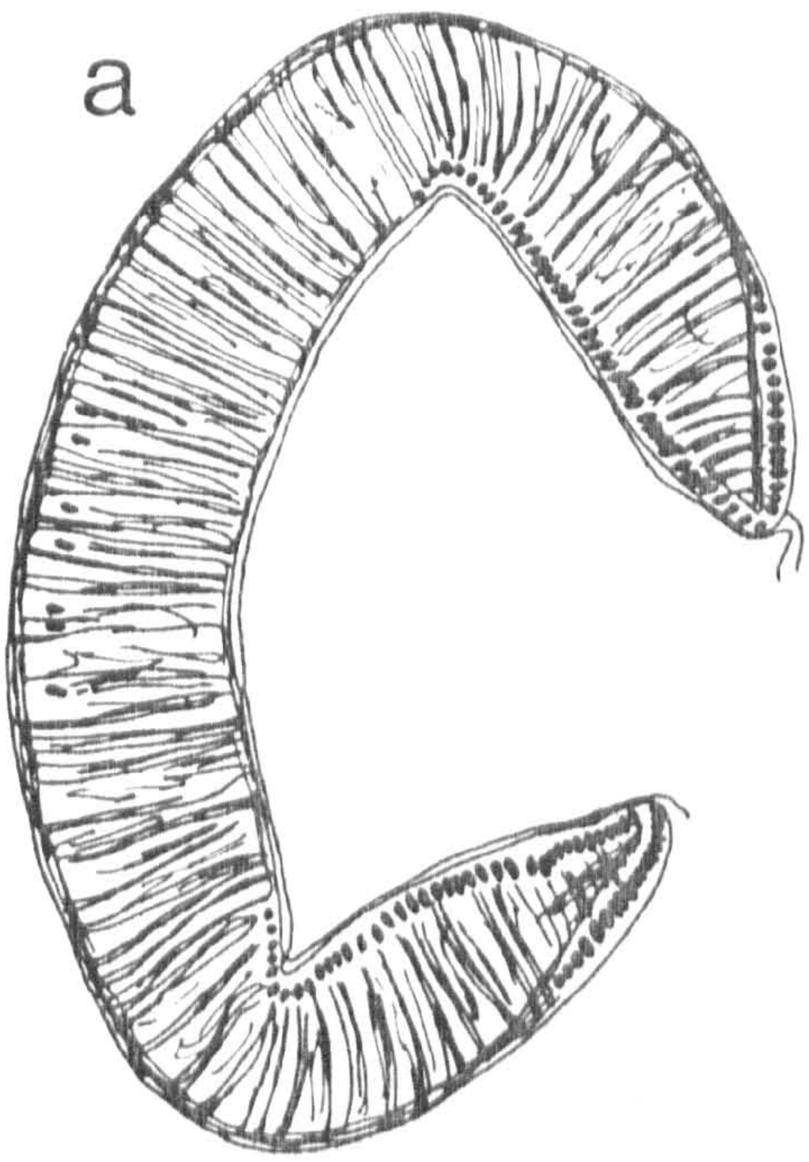
(median sagittal section)

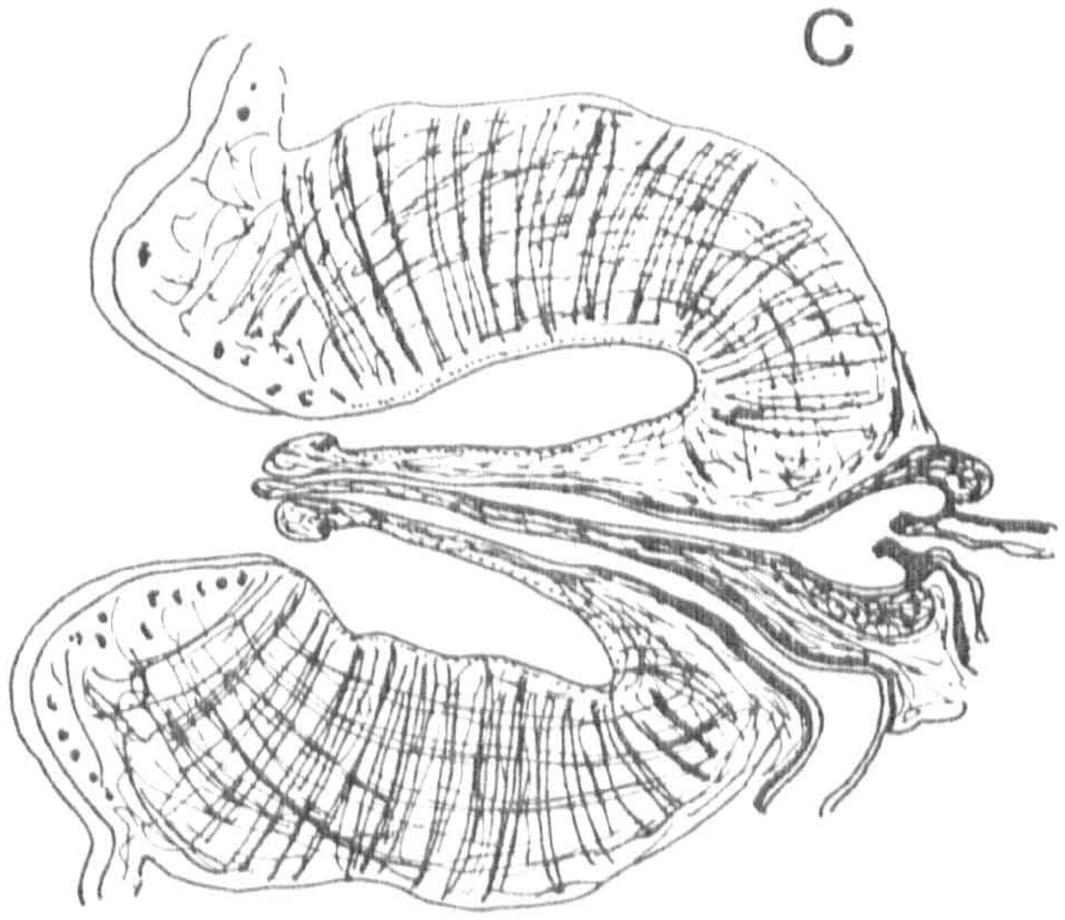
a. Acetabulum (cotylophoron type)

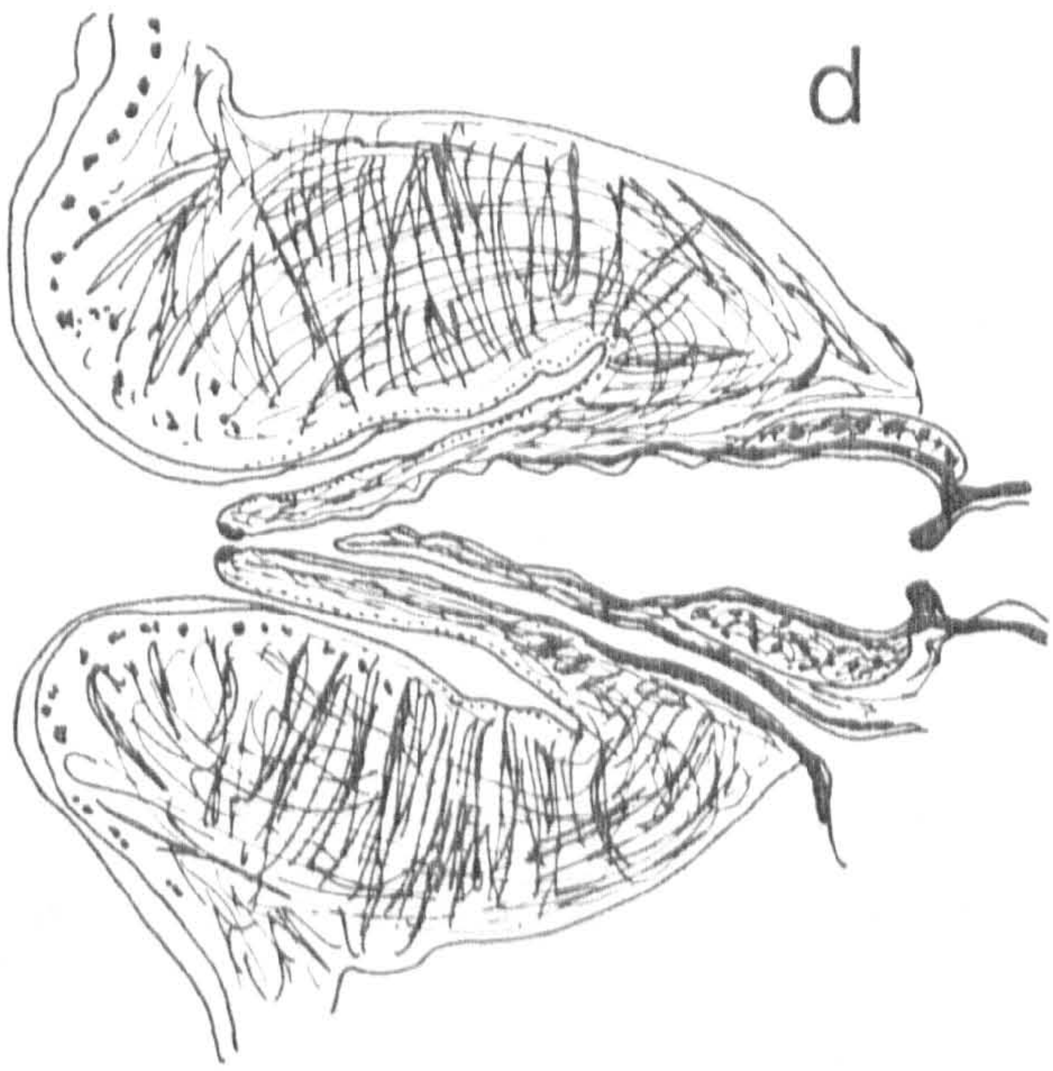
b. Pharynx (calicophoron type) and oesophagus, note thick musculature of wall of oesophagus.

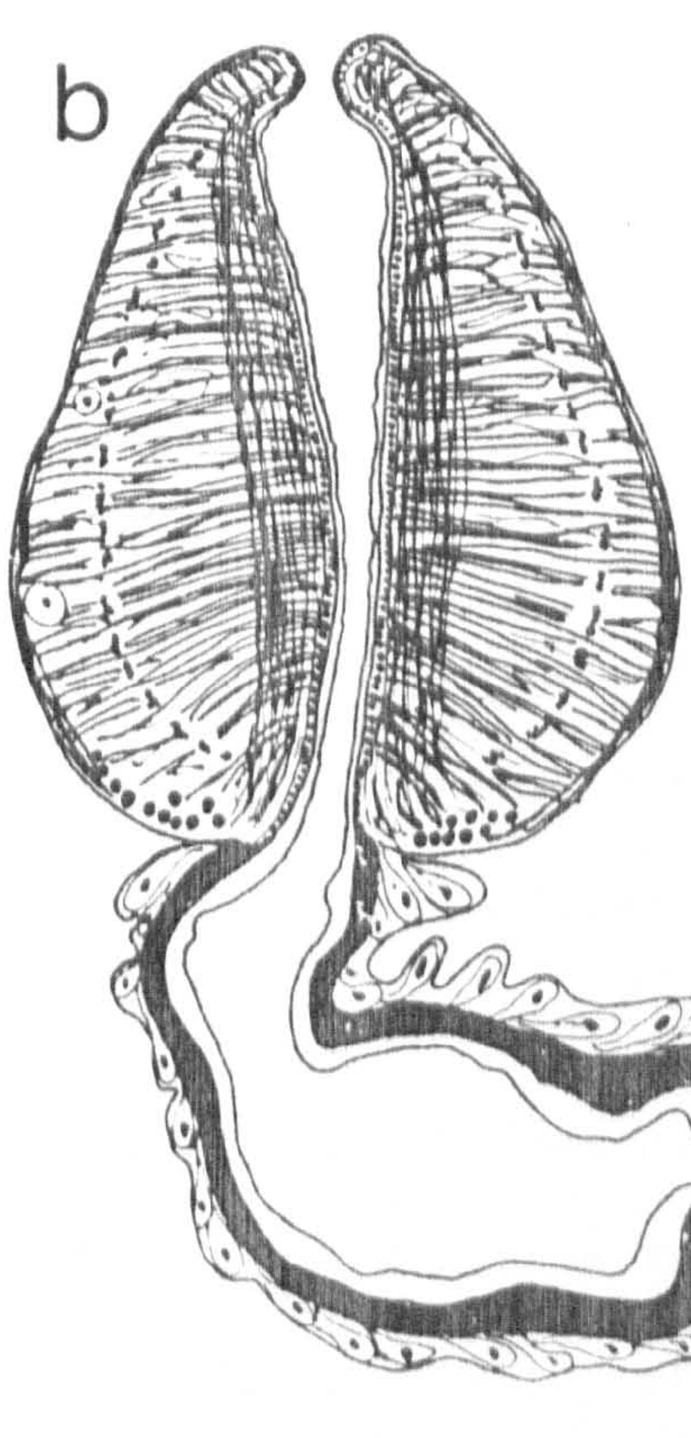
c. Terminal genitalium (cotylophoron type)

d. Another terminal genitalium (cotylophoron type)









0.5mm a

0.4 mm b,c,d

Cotylophoron fuelleborni Näsmark, 1937

Synonyms: Cotylophoron indicum of Näsmark, 1937
Cotylophoron noveboracensis Price and McIntosh, 1953

TYPE SPECIMENS: Museum für Naturkunde (Bereich Zoologisches Museum) an der Alexander von Humboldt Universität zu Berlin (Coll. No. 6446) from Bubalus caffer nanus in Cameroon.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Cattle	Kenya	London School of Hygiene & Tropical Medicine
	Mazabuka, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Buffalo	Fort Jameson, Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L LeRoux collection.
	?	London School of Hygiene & Tropical Medicine coll. no. 2011.

HABITAT: Rumen

DESCRIPTION:

Body small, conical, may bend slightly ventrally, usually rounded anteriorly and posteriorly, 3.30-5.79 mm long, 1.52-2.37 mm in the dorso-ventral direction.

Acetabulum subterminal, 1.05-1.56 mm in external diameter in the dorso-ventral direction; ratio to body length 1:2.9 to 1:3.8; of the cotylophoron type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 12-19; d.i.c., 30-38; v.e.c., 10-15; v.i.c., 31-39; m.e.c., 7-12.

Pharynx 0.47-0.68 mm long, 0.42-0.56 mm in the dorso-ventral direction; ratio to body length 1:6.1 to 1:7.6, to the diameter of the acetabulum 1:1.8 to 1:2.3; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section; internal surface has small dome-shaped papillae. Oesophagus 0.30-0.52 mm long, muscu-lature of wall relatively thin and more or less uniform in thickness, no bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form about six dorso-ventral bends, reach level of acetabulum with the blind ends directed dorsally.

Testes lobed, directly or obliquely tandem in posterior half of the body; anterior testis 0.40-0.56 mm long, 0.85-1.13 mm in the dorso-ventral direction; posterior testis 0.47-0.60 mm long, 0.77-1.18 mm in the dorso-ventral direction. Seminal vesicle thin-walled and strongly coiled; pars musculosa thick-walled, well developed and convoluted; pars prostatica small and weakly developed.

Ovary subspherical, 0.21-0.33 by 0.20-0.32 mm, posterior to testes and dorsal to acetabulum; Mehlis' gland close to ovary, either anterior to or at level of it, 0.20-0.22 by 0.19-0.25 mm; Laurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface about 0.30-0.41 mm posteriorly to the excretory pore; uterus winds forward, dorsal to the testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of the oesophageal bifurcation to the acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 120-140 by 55-65 µm.

Genital pore opens on the ventral surface at level of the oesophageal bifurcation or posterior to it; terminal genitalium of the cotylophoron type (sensu Näsmark, 1937) in median sagittal section; genital sucker 0.50-0.68 mm in diameter, slightly smaller or as large as the pharynx, ratio to the diameter of the acetabulum 1:1.7 to 1:2.2.

Excretory vesicle dorsal to acetabulum, ovary, Mehlis' gland and posterior testis; excretory pore opens on the dorsal surface at level of posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 128

Cotylophoron fuelleborni Näsmark, 1937

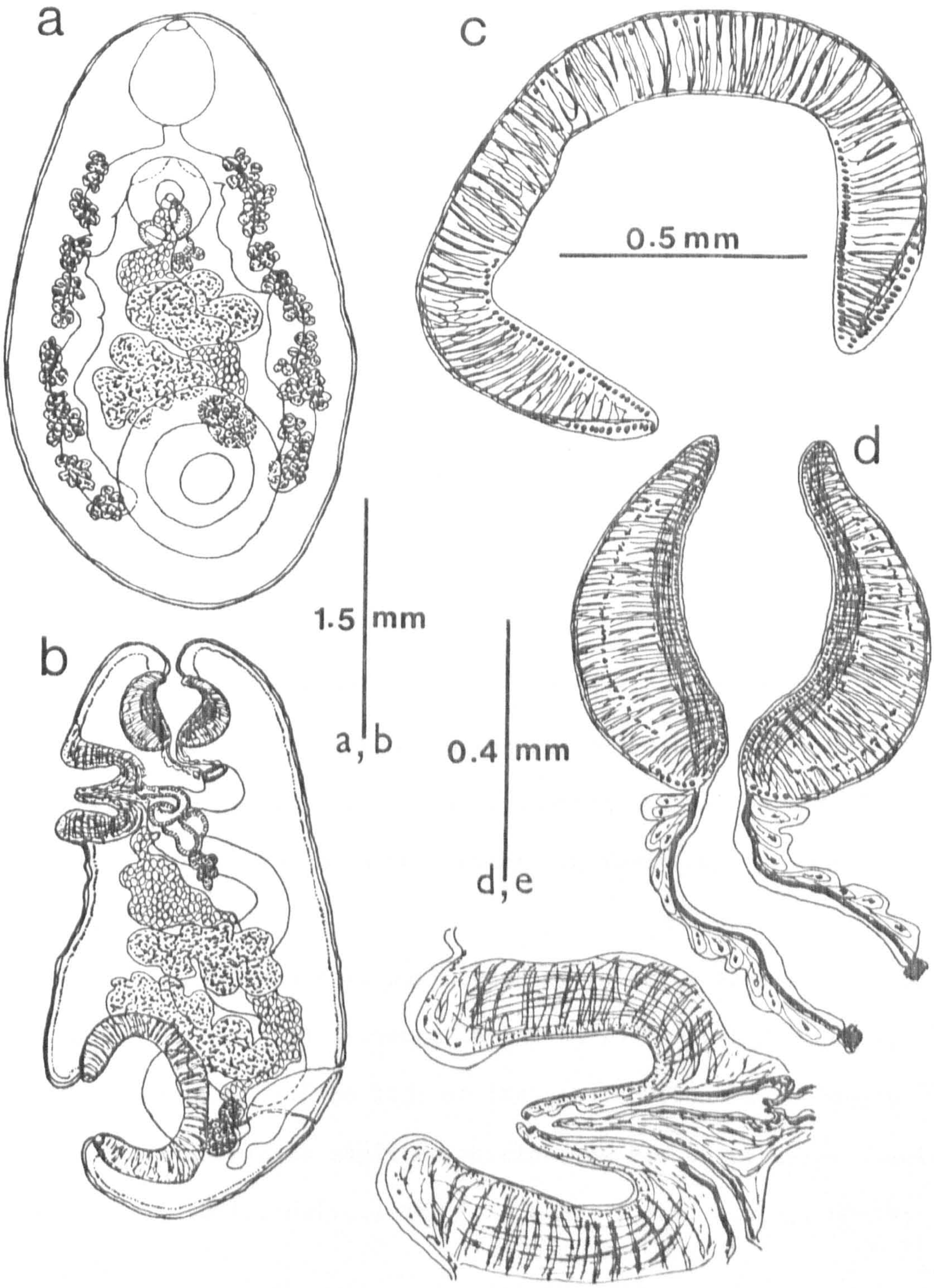
a. Whole worm, ventral view

b. Whole worm, sagittal view

c. Acetabulum (cotylophoron type),median sagittal section

c. Pharynx (calicophoron type) and oesophagus, median sagittal section

d. Terminal genitalium (cotylophoron type), median sagittal section


a
c
0.5 mm
d
1.5 mm
a, b
b
0.4 mm
d, e
e

Cotylophoron panamensis Price and McIntosh, 1953

TYPE SPECIMENS: United States National Parasite Collection, USDA, Beltsville, Maryland (USNMH Coll. No. 45441) from the first stomach of sheep (Ovis aries) in Panama.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collection

Bos taurus	Carimagua, Llanos Orientalis, Columbia	Dr. Fabio Nelson Suluaga
	Cuba	Dr. J. Prokopič
	Nagua, Provincia de Maria Trinidad Sanchez, Dominican Republic	Dr. Jesus M. Alvares

HABITAT: Rumen

DESCRIPTION:

Body conical, slightly flattened and curved ventrally, 3.60-5.92 mm long, 2.73-4.08 mm in the dorso-ventral direction; body surface has papillae around oral opening and on the rim of the genital sucker, those on the latter are fewer and randomly arranged.

Acetabulum subterminal, surrounded by folds in some specimens, 1.56-2.03 mm in external diameter in the dorso-ventral direction; ratio to body length 1:2 to 1:3; of the cotylophoron type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 12-17; d.i.c., 46-57; v.e.c., 10-15; v.i.c., 50-59; m.e.c., 7-12.

Pharynx 0.43-0.97 mm long, 0.40-0.80 mm in the dorso-ventral direction; ratio to body length 1:5 to 1:6.3, to the diameter of the acetabulum 1:1.8 to 1:2; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section; internal surface lined by small dome-shaped papillae. Oesophagus 0.50-0.72 mm long, musculature of wall moderate in thickness, no bulb or posterior sphincter, lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form five dorso-ventral bends, reach level of acetabulum with the blind ends directed dorsally.

Testes deeply lobed, usually juxtaposed but sometimes obliquely horizontal in middle third of the body; right testis 0.93-1.57 mm long, 1.20-2.86 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa thick-walled, well developed and convoluted; pars prostatica small and weakly developed.

Ovary subspherical, 0.26-0.53 by 0.48-0.62 mm, posterior to testes and dorsal to acetabulum; Mehlis' gland close to ovary, 0.38-0.49 by 0.44-0.57 mm; Laurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface about 0.32-0.58 mm posteriorly to the excretory pore; uterus winds forward, dorsal to the testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of pharynx to acetabulum, confluent dorso-medially in their posterior limit; egg 128-132 by 58-60 µm.

Genital pore opens on the ventral surface at a level posterior to the oesophageal bifurcation; terminal genitalium of the cotylophoron type (sensu Näsmark, 1937) in median sagittal section; genital sucker 0.45-0.75 mm in diameter, slightly smaller than the

pharynx, ratio to the diameter of the acetabulum 1:2.5 to 1:3.4.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface anteriorly to the Laurer's canal opening.

FIGURE 129

Cotylophoron panamensis Price and McIntosh, 1953

(SEM)

a. Whole worm, ventral view (scale bar = 500 µm)

b. Acetabular region (scale bar = 300 µm)

c. Anterior end, note papillae around oral opening (scale bar = 100 µm)

d. Genital pore region with genital papilla partly out (scale bar = 100 µm)

e. Another genital pore region (scale bar = 100 µm)

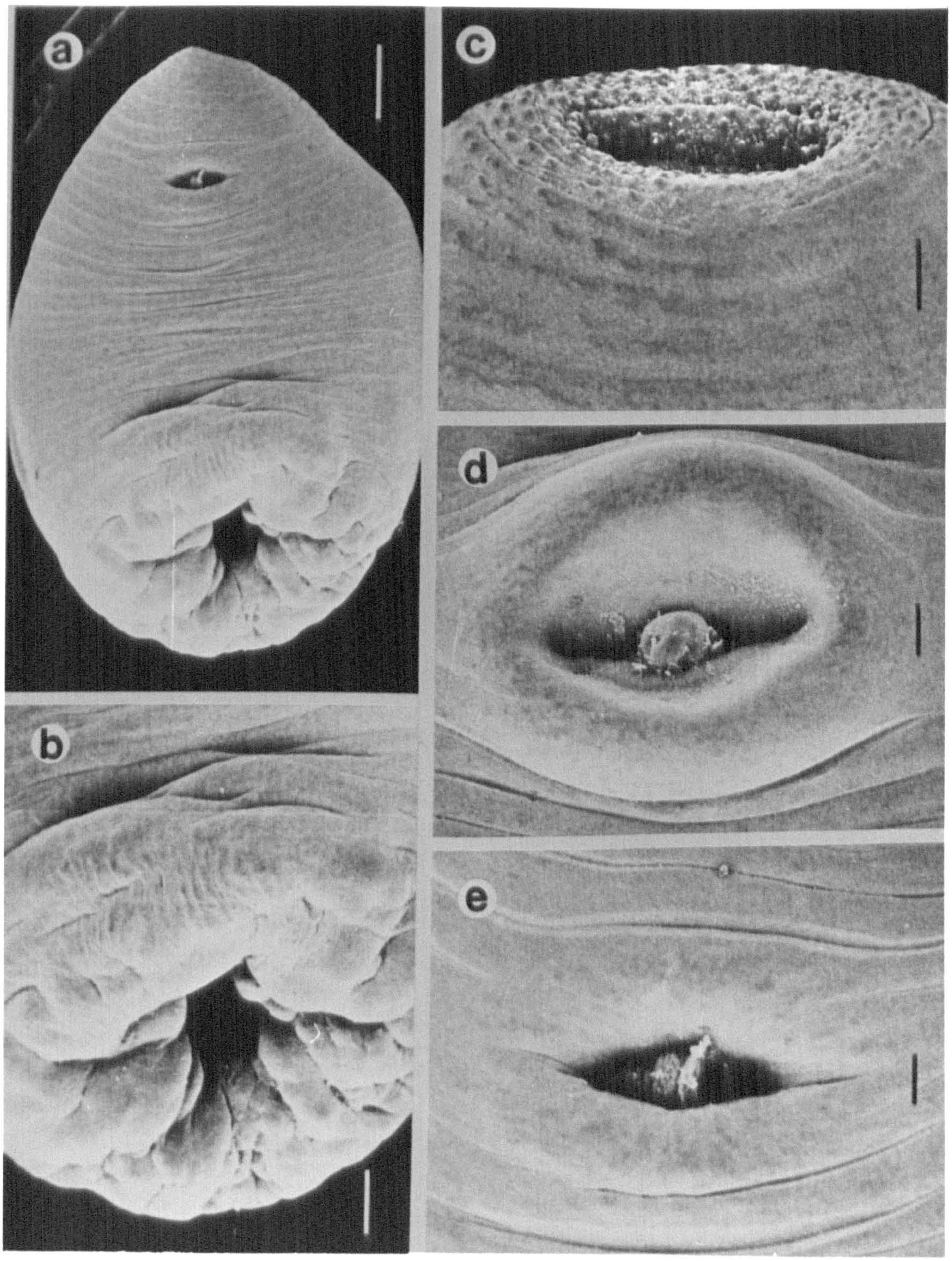

a
b
c
d
e

FIGURE 130

Cotylophoron panamensis Price and McIntosh, 1953

a. Whole worm, ventral view

b. Whole worm, sagittal view

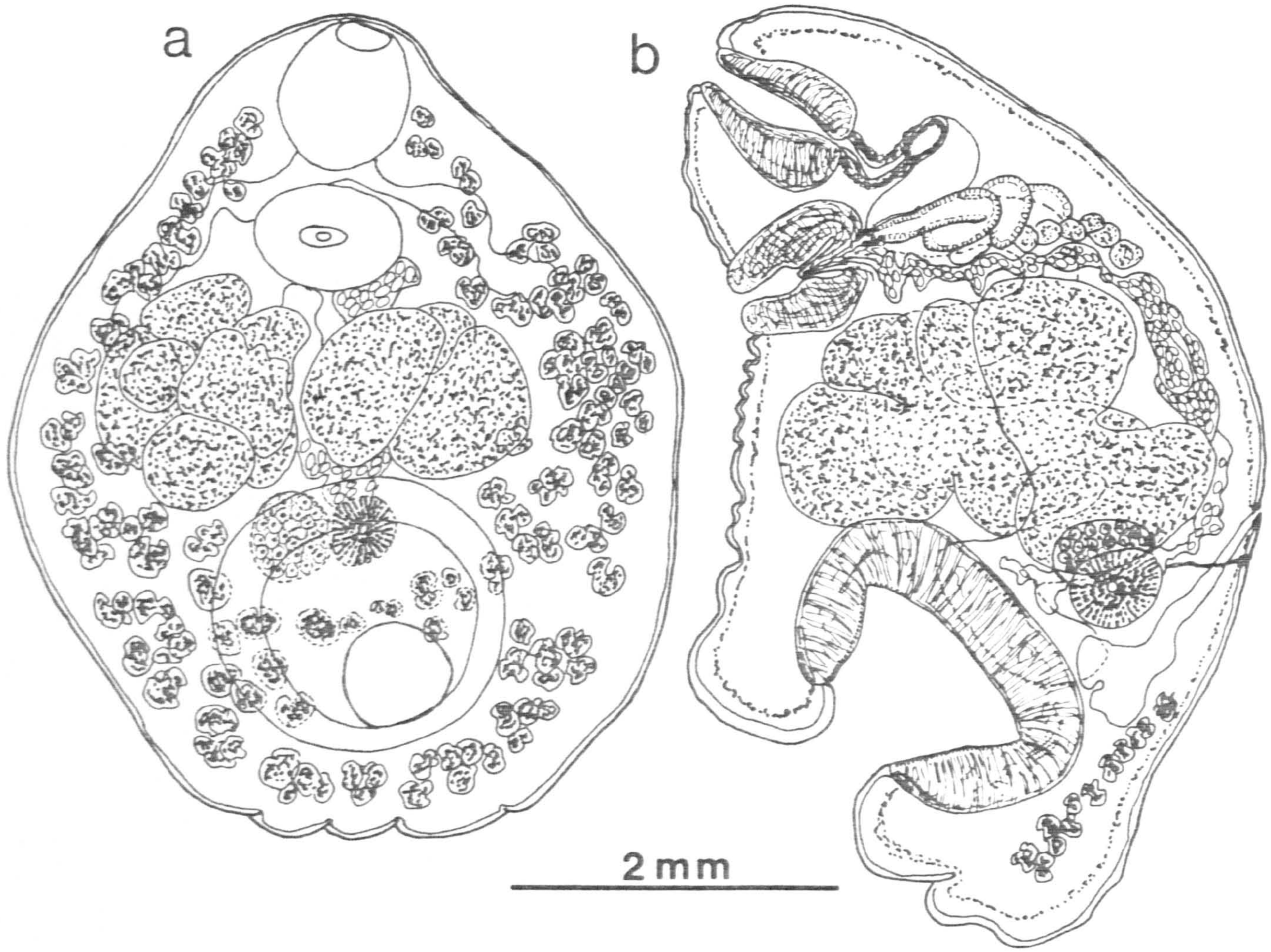

a
b
2 mm

FIGURE 131

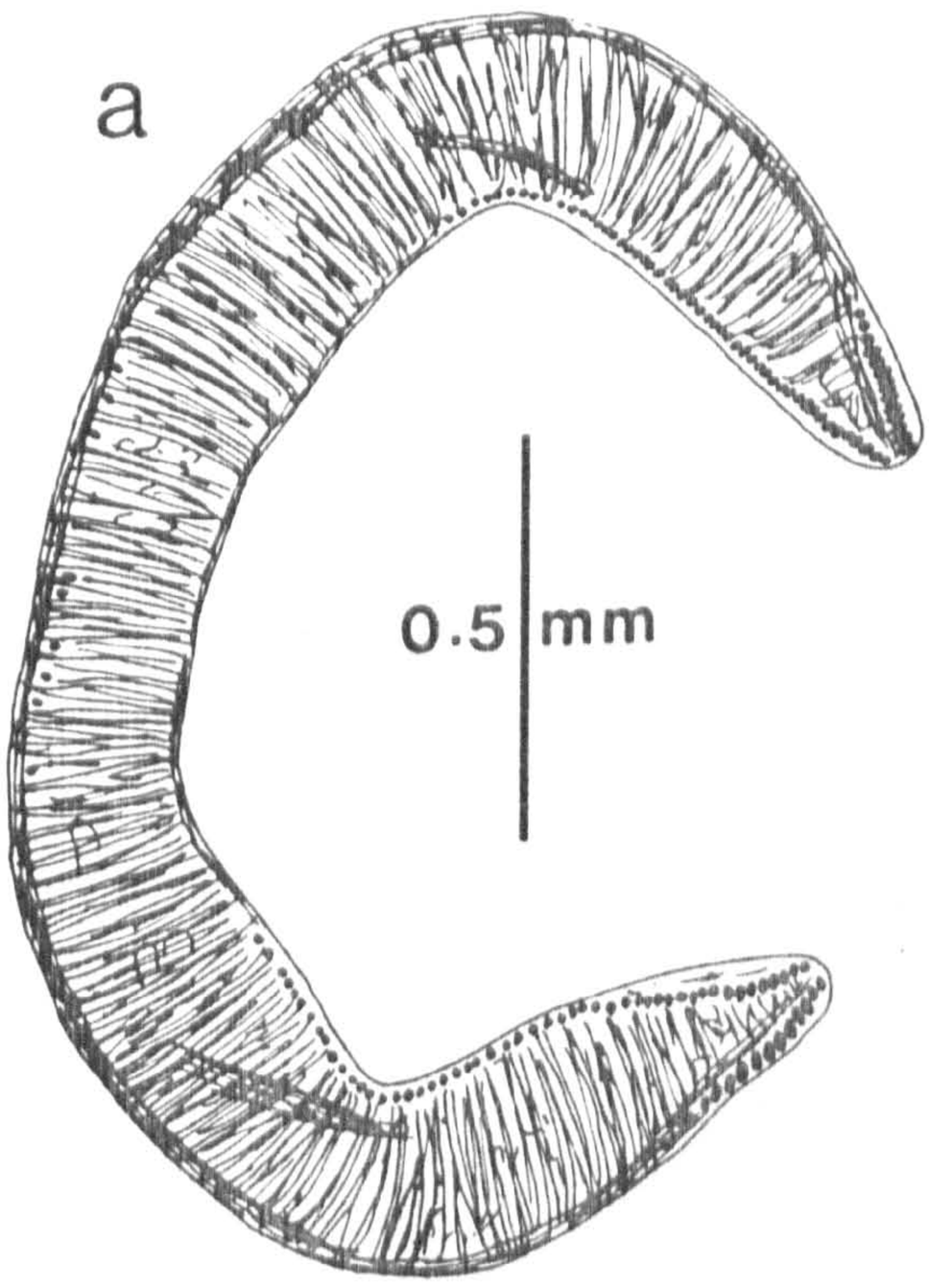
Cotylophoron panamensis Price and McIntosh, 1953

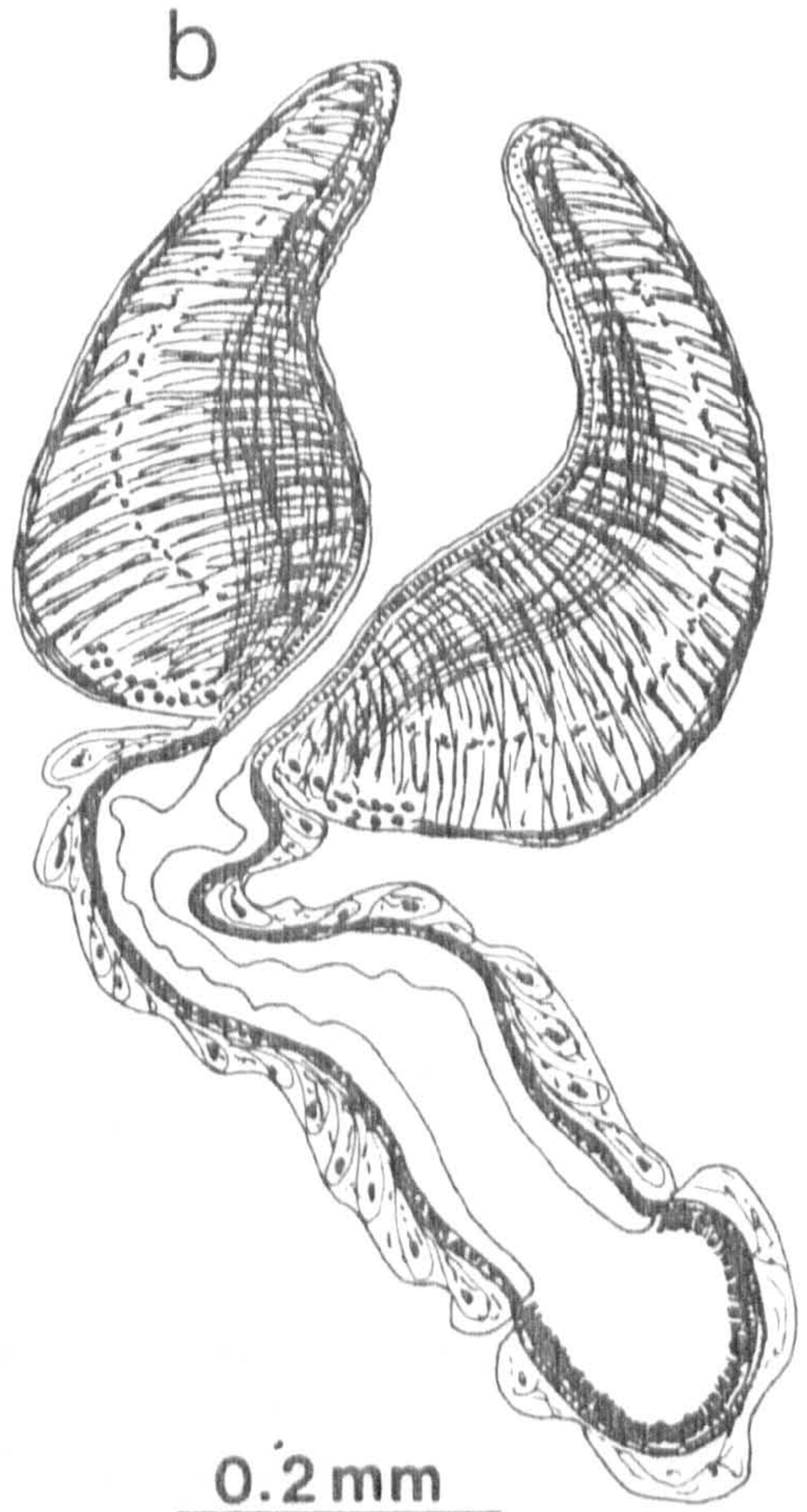
(median sagittal section)

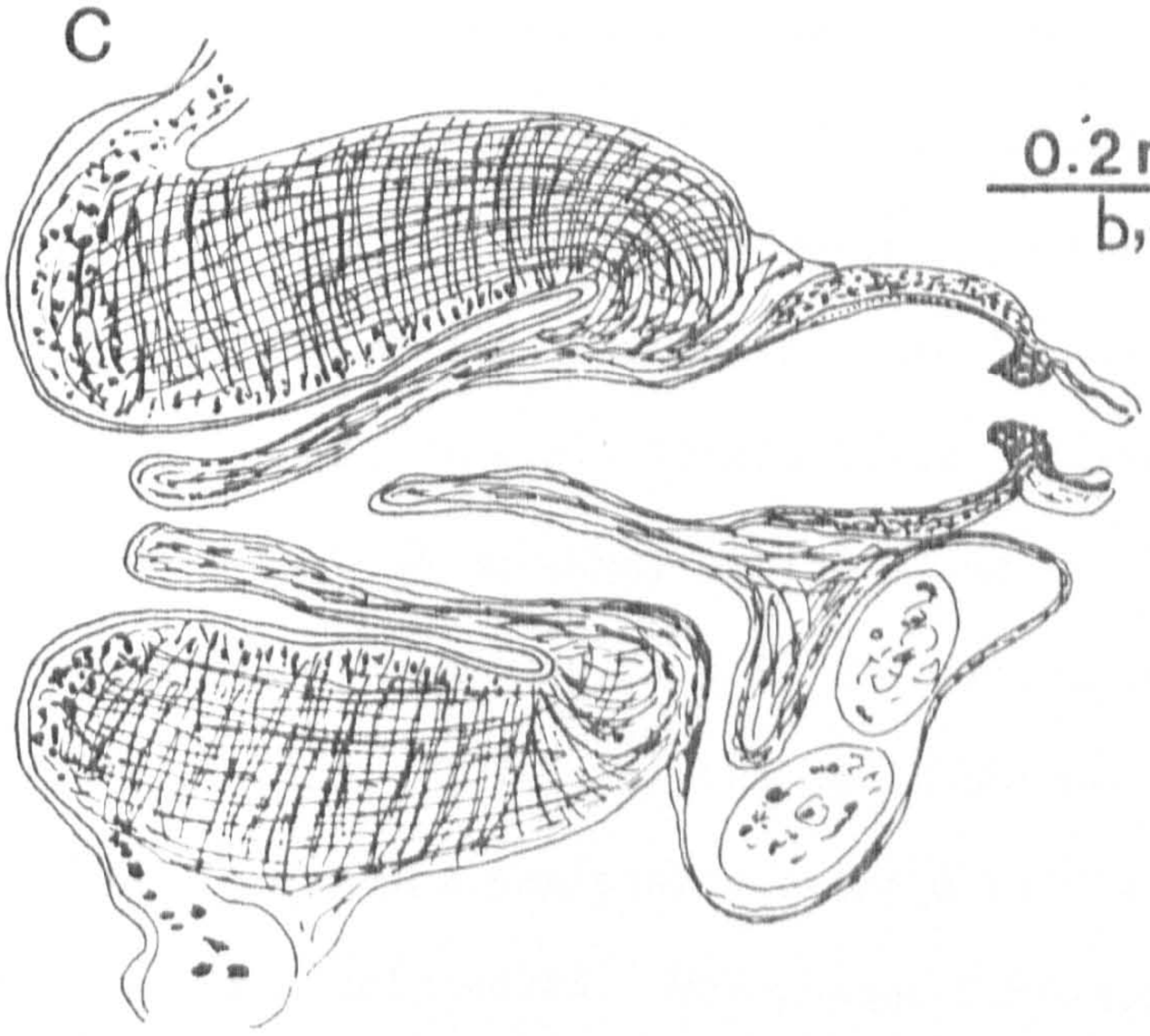
a. Acetabulum (cotylophoron type)

b. Pharynx (calicophoron type) and oesophagus

c. Terminal genitalium (cotylophoron type)


a
0.5 mm


b
0.2 mm
b,c


C

Cotylophoron bareilliense Mukherjee and Chauhan, 1965

Synonym: Cotylophoron skrjabini Mukherjee, 1963

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collection

Bos indicus	Mahiyangana, Kandy Area, Sri Lanka	Commonwealth Institute fo Helminthology, Dr. J.A. Dinnik collection.
Bos taurus	Iloilo, Philippines	Author's own collection
Bubalus bubalis	Pangasinan, Philippines	Author's own collection

HABITAT: Rumen

DESCRIPTION:

Body conical, almost straight but may bend slightly ventrally, 5.01-9.78 mm long, 2.72-3.46 mm in the dorso-ventral direction. Body surface has dome-shaped papillae around the oral opening.

Acetabulum subterminal, moderate in size, 1.43-1.84 mm in external diameter in the dorso-ventral direction; ratio to body length 1:4 to 1:5.3; of the cotylophoron type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 12-26; d.i.c., 45-62; v.e.c., 10-22; v.i.c., 47-56; m.e.c., 3-9.

Pharynx 0.52-0.84 mm long, 0.51-0.82 mm in the dorso-ventral direction; ratio to body length 1:10 to 1:11.5, to the diameter of the acetabulum 1:2 to 1:2.4; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section with few and weakly developed middle circular muscle units. Oesophagus 0.96-1.08 mm long, musculature of wall relatively thin, no bulb or posterior sphincter,

lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form about five dorso-ventral bends, reach level of acetabulum with the blind ends directed dorsally.

Testes small, lobed, obliquely tandem in posterior two third of the body; anterior testis 0.21-0.50 mm long, 0.30-0.79 mm in the dorso-ventral direction; posterior testis 0.22-0.61 mm long, 0.27-0.74 mm in the dorso-ventral direction. Seminal vesicle thin-walled and strongly coiled; pars musculosa thick-walled, well developed and convoluted; pars prostatica small and weakly developed.

Ovary subspherical, larger than testes, 1.00-1.14 by 0.78-1.06 mm; Mehlis' gland close to ovary, 0.50-0.57 by 0.55-0.66 mm; Laurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface about 0.26-0.45 mm posteriorly to the excretory pore; uterus winds forward, dorsal to the testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of the oesophageal bifurcation to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 105-161 by 61-81 µm.

Genital pore opens on the ventral surface at a level posterior to the oesophageal bifurcation; of the cotylophoron type (sensu Näsmark, 1937) in median sagittal section; genital sucker 0.53-0.89 mm in diameter, slightly smaller or as large as the pharynx, ratio to the diameter of the acetabulum 1:1.7 to 1:2.4.

Excretory vesicle antero-dorsal to acetabulum and dorsal to ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level of the ovary and anteriorly to the Laurer's canal opening.

FIGURE 132

Cotylophoron bareilliense Mukherjee and Chauhan, 1965

a. Whole worm, ventral view

b. Whole worm, sagittal view

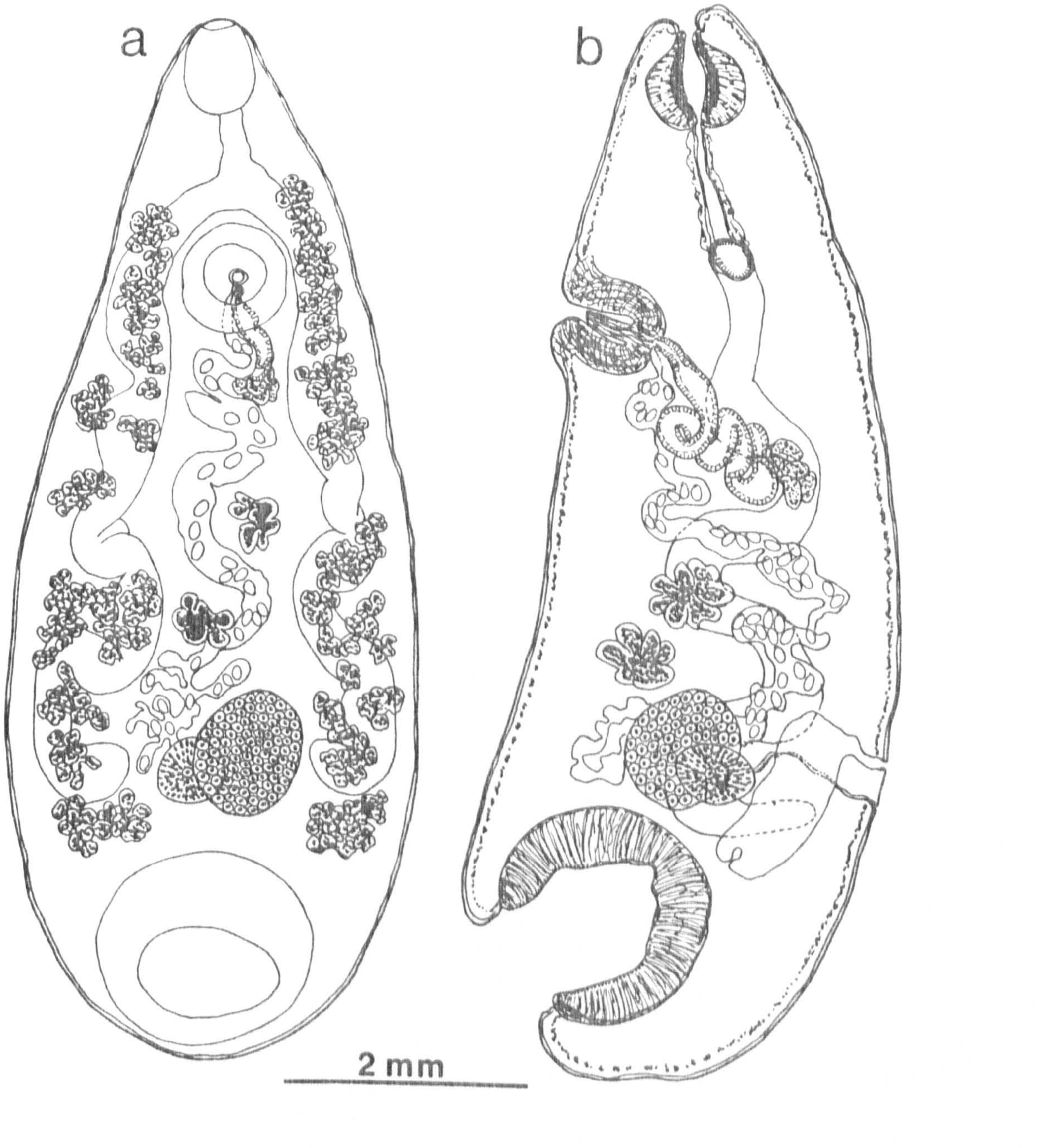

a
b
2 mm

FIGURE 133

Cotylophoron bareilliense Mukherjee and Chauhan, 1965

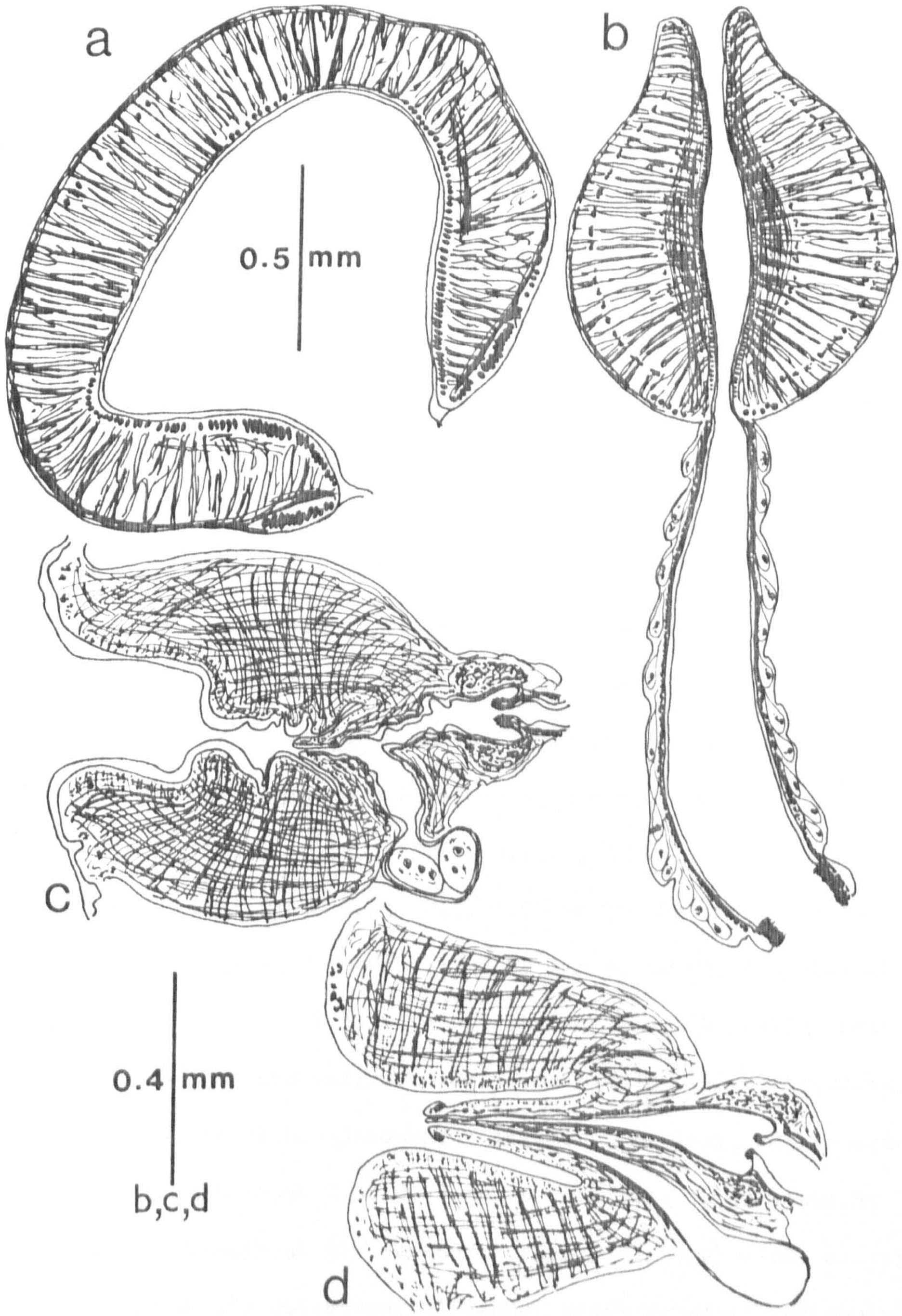
(median sagittal section)

a. Acetabulum (cotylophoron type)

b. Pharyns (calicophoron type) and oesophagus

c. Terminal genitalium (cotylophoron type), with retracted genital papilla.

d. Terminal genitalium (cotylophoron type), relaxed form.


a
0.5 mm
b
C
0.4 mm
b,c,d
d

Cotylophoron macrosphinctris Sey and Graber, 1979

TYPE SPECIMENS: Not examined

MATERIALS EXAMINED: Hosts, localities and donors/collection

Syncerus caffer	Acholi, Uganda	Loaned by Dr. J.A. Dinnik
	Parc National de la Garamba, Zaire	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.

HABITAT: Rumen

DESCRIPTION:

Body conical, nearly straight, 5.41-7.82 mm long, 2.30-3.05 mm in the dorso-ventral direction. Body surface has papillae which are very small and present only on the rim of the genital sucker and around the acetabular opening.

Acetabulum subterminal, 1.19-2.05 mm in external diameter in the dorso-ventral direction; ratio to body length 1:4 to 1:4.7; of the cotylophoron type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.. 10-15; d.i.c., 47-50; v.e.c., 11-15; v.i.c., 43-48; m.e.c., 12-17.

Pharynx 0.78-1.23 mm long, 0.57-1.03 mm in the dorso-ventral direction; ratio to body length 1:7.8 to 1:8.6, to the diameter of the acetabulum 1:2 to 1:2.5; internal surface lined by small dome-shaped papillae; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section. Oesophagus 1.15-1.52 mm long, with muscular posterior bulb about 0.38-0.49 mm in diameter, lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form about six dorso-ventral bends, reach level of acetabulum with the blind ends directed dorsally.

Testes lobed, obliquely tandem in posterior two third of the body; anterior testis 0.41-1.82 mm long, 1.23-1.62 mm in the dorso-ventral direction; posterior testis 0.52-1.85 mm long, 1.10-1.92 mm in the dorso-ventral direction. Seminal vesicle thin-walled and strongly coiled; pars musculosa thick-walled, well developed and convoluted; pars prostatica small and weakly developed.

Ovary subspherical, 0.28-0.68 by 0.76-0.96 mm; Mehlis' gland close to ovary, 0.57-0.66 by 0.50-0.55 mm; Laurer's canal crosses the excretory vesicle or duct and opens on the dorsal surface about 0.56-0.69 mm posteriorly to the excretory pore; uterus winds forward, dorsal to the testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of oesophagus to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 100-151 by 60-73 µm.

Genital pore opens on the ventral surface at a level posterior to the oesophageal bifurcation; terminal genitalium of the schistocotyle type (sensu Sey and Graber, 1979a); genital sucker 1.09-1.34 mm, slightly larger than the pharynx, ratio to the diameter of the acetabulum 1:1.4 to 1:1.5.

Excretory vesicle antero-dorsal to acetabulum, dorsal to ovary and Mehlis' gland; excretory pore opens on the dorsal surface at level of the posterior testis and anteriorly to the Laurer's canal opening.

FIGURE 134

Cotylophoron macrosphinctris Sey and Graber, 1979

(SEM)

a. Whole worm, ventral view (scale bar = 300 µm)

b. Acetabular region (scale bar = 200 µm)

c. Anterior end (scale bar = 100 µm)

d. Genital pore region with genital papilla everted
(scale bar = 100 µm)

e. Genital pore region with genital papilla retracted
(scale bar = 100 µm)

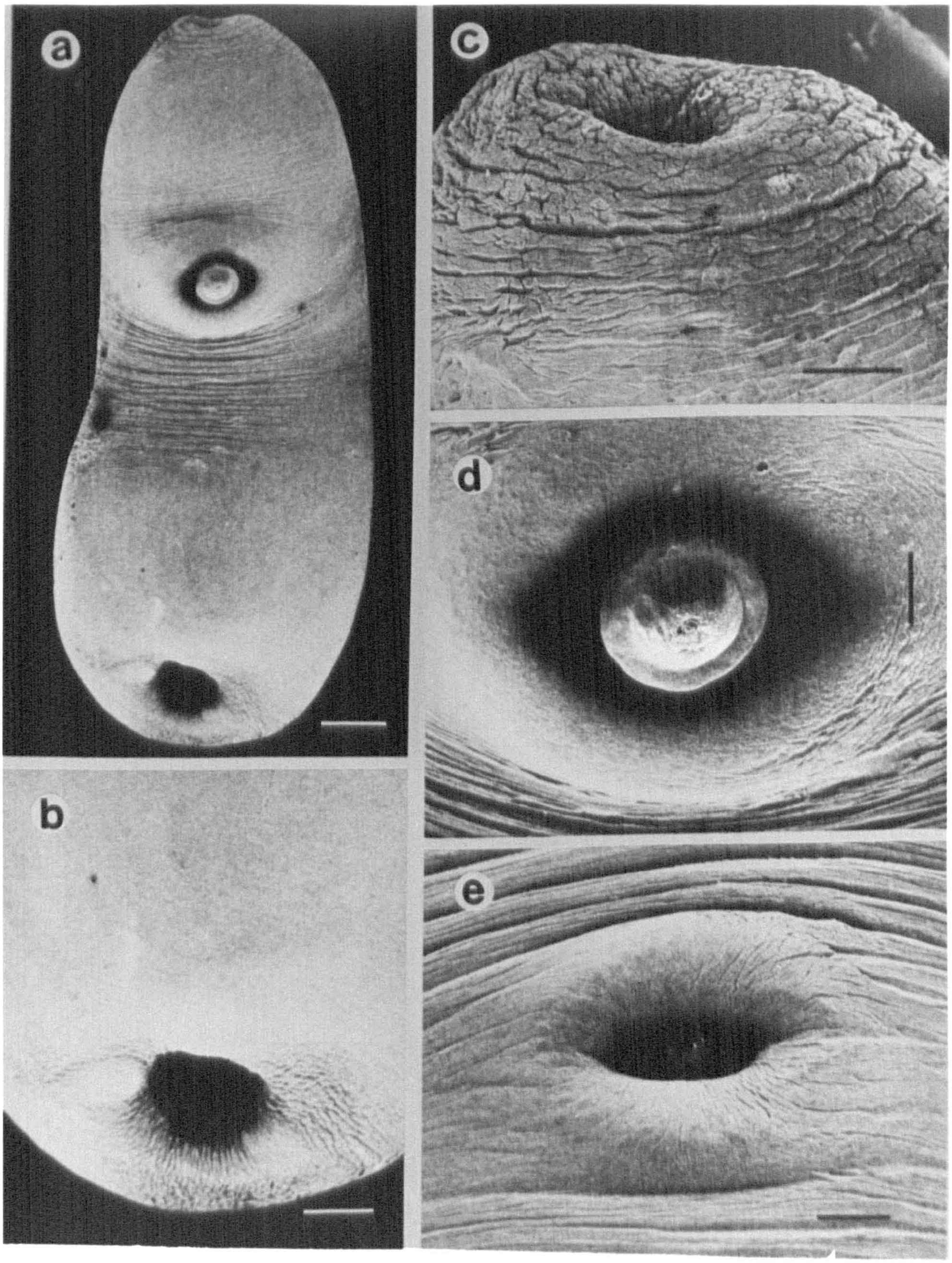

a
c
d
b
e

FIGURE 135

Cotylophoron macrosphinctris Sey and Graber, 1979

Whole worm, sagittal view

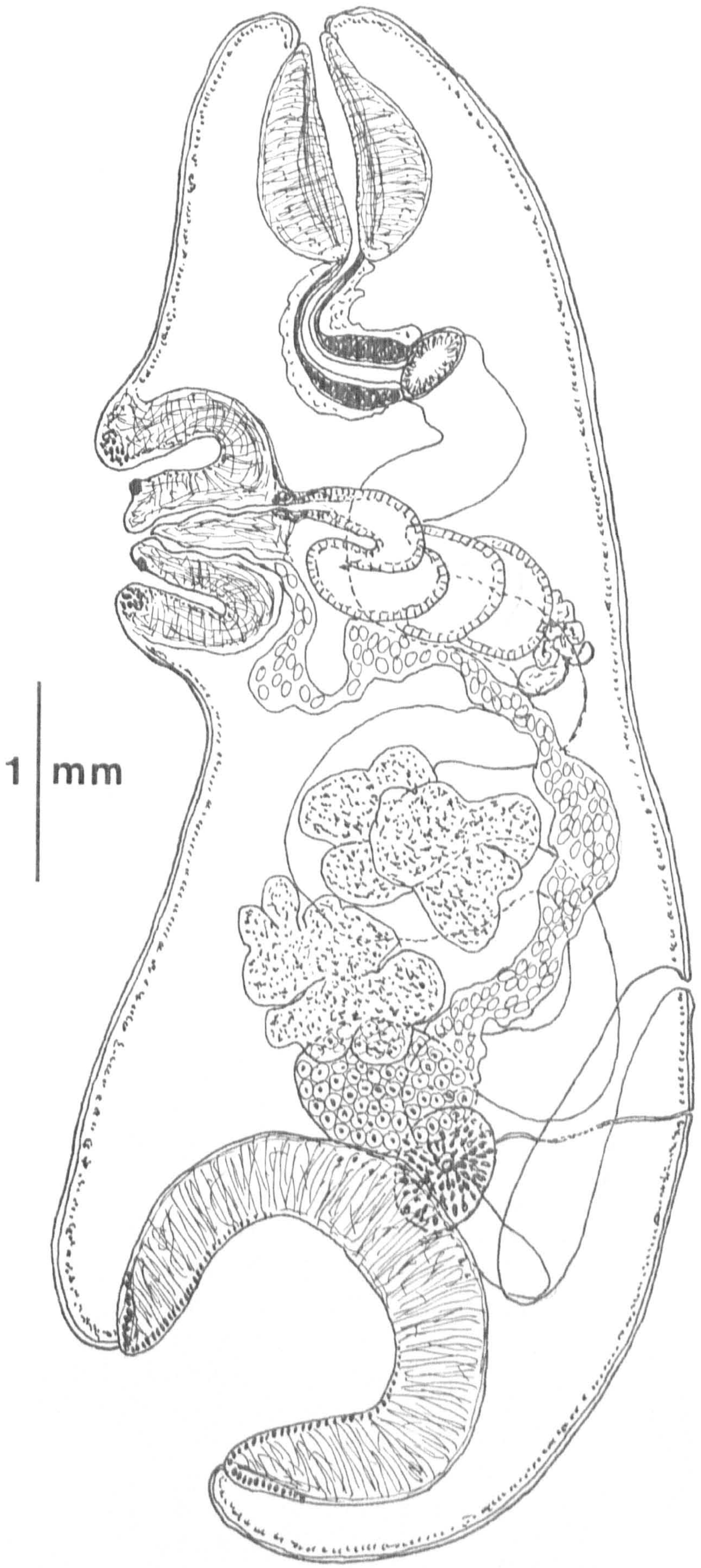

1 mm

FIGURE 136

Cotylophoron macrosphinctris Sey and Graber, 1979

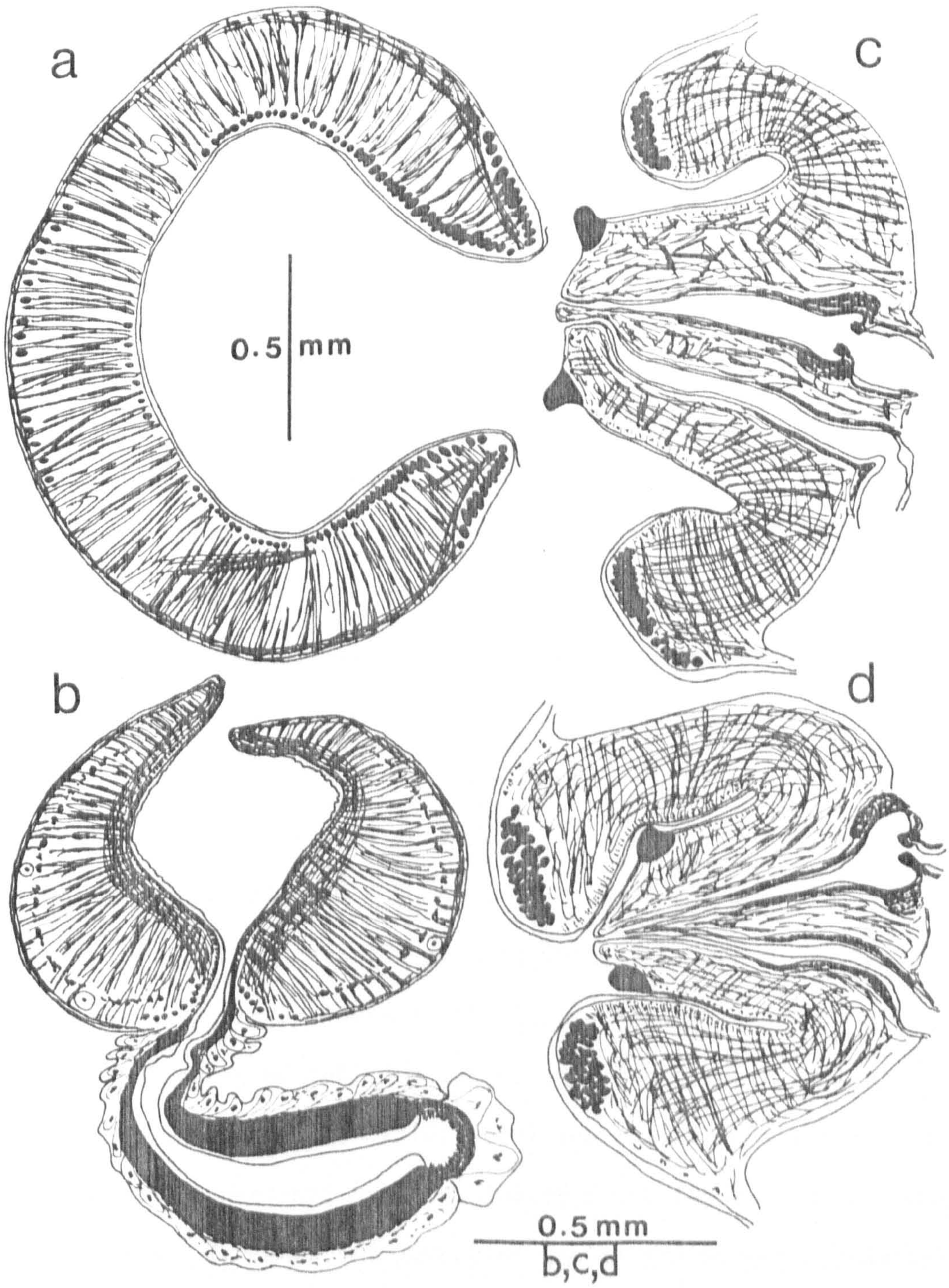
(median sagittal section)

a. Acetabulum (cotylophoron type)

b. Pharynx (calicophoron type) and oesophagus, note muscular posterior bulb.

c. Terminal genitalium (schistocotyle type), note sphincter on rim of sucker, relaxed form.

d. Another terminal genitalium (schistocotyle type), retracted form.


a
0.5 mm
c
b
d
0.5 mm
b,c,d

Cotylophoron xiangjiangense Wang, 1979

TYPE SPECIMENS: Not examined. No other material was available for examination.

HOST: Bubalus bubalis

LOCALITY: Wu Lan, China

HABITAT: Stomach

DESCRIPTION: (Adapted and translated from the author's description which is in Chinese and re-arranged to conform to the format of description of the rest of the species given in this work).

Body long, oval, slightly bent ventrally, about 3.85-5.60 mm long, 1.93-3.05 mm wide at the region of the testes.

Acetabulum 1.23-1.72 by 1.23-1.58 mm; ratio to body length 1:3 to 1:3.2; wall 0.414 mm thick; radial fibres well developed, grouped to form muscle bundles; exterior longitudinal muscle fibres not developed; exterior circular series narrow but units are well developed than those in the interior circular series; number of circular muscle units, d.e.c.1, 16; d.e.c.2, 14; d.i.c., 55; v.e.c., 18; v.i.c., 63, close to the paramphistomum type.

Pharynx oval, 0.437-0.787 mm long, 0.560-0.787 mm wide; ratio to body length 1:9.8; anterior part of internal surface has papillae; interior circular layer occupies the length along the inner wall; middle circular series well developed; exterior circular series at a distance from the middle series but joins the latter at the anterior one third of the pharynx; interior longitudinal layer distinct and well developed; anterior and posterior sphincters absent; close to the liorchis type. Oesophagus about 0.672 mm long, with muscular posterior bulb; wall 0.007 mm thick anteriorly, 0.034 mm thick

posteriorly. Caeca in lateral sides of the body, form dorso-ventral bends, reach level of posterior border of acetabulum.

Testes oval, tandem or diagonal in middle of the body; anterior testis 0.719 by 0.573 mm; posterior testis 0.766 by 0.737 mm; pars musculosa thick-walled and forms four to five convolutions; pars prostatica short.

Ovary left of posterior testis, 0.373 by 0.403 mm; vitellaria in lateral fields, extend from level of posterior part of oesophagus to posterior border of acetabulum; egg 115-140 by 63-80 µm.

Genital pore at level of oesophageal bifurcation; genital sucker 0.525-0.613 by 0.525-0.640 mm; ratio to pharynx 1:1.2, radial fibres strongly developed; belongs to the cotylophoron type.

Excretory vesicle bag-shaped, crossed by Laurer's canal and opens anteriorly to the opening of the latter.

DISCUSSION

Näsmark (1937) has placed considerable emphasis on the shape and length of the body, disposition of the testes and the ratio of the body length in relation to other organs as features in separating species of the genus. Some authors seemed to have accepted the scheme strictly without giving allowance for variations and this resulted in the description of new species based on slight differences in body shape and size, organ measurements and organ ratios.

Prudhoe (1957) has shown that the majority of the numerous specimens of C. cotylophorum he examined from Africa have testes disposed in tandem but very contracted specimens have diagonally or sometimes even symmetrically arranged testes. It was observed in this study that in most species in the genus, the disposition of the testes may vary from directly tandem to obliquely tandem except in one species, C. panamensis where the testes normally are juxtaposed and very rarely may be obliquely horizontal in position. It was also observed that body shape may vary from short and broad to more elongate and narrow depending on the state of relaxation of the worm during fixation. Consequently, the length of the body as well as any ratio obtained in relation to it may also vary considerably.

Maplestone (1923), Dollfus (1950) and Prudhoe (1957) did not regard the presence of an oesophageal bulb among Cotylophoron species as a constant specific character. Näsmark (1937) however has shown that the specimens from which Maplestone based his observation actually consisted of more than one species and that

the presence of an oesophageal bulb is a specific character. It was also observed in this study that the presence of an oesophageal bulb is a constant feature in the species, C. cotylophorum and C. macrosphinctris but absent in the remaining species of the genus.

Näsmark (1937) has accepted the validity of Cotylophoron indicum Stiles and Goldberger, 1910 without examining the type specimens and redescribed it based on new materials from cattle in the Sudan. Dinnik, Walker, Barnett and Brocklesby (1963) reported the species from Syncerus caffer in western Uganda. The writer has re-examined Näsmark's original material of C. indicum loaned from the Naturhistoriska riksmuseet, Stockholm (RMev. Sthlm. Coll. No. 2959) and the specimens are not identical with the type of C. indicum Stiles and Goldberger, 1910. In fact, they are similar to C. fuelleborni except for their large size but the difference is not great enough to justify the separation of the two. Cotylophoron indicum of Näsmark, 1937 therefore is regarded here as a synonym of C. fuelleborni Näsmark, 1937. The specimens identified by Dinnik, Walker, Barnett and Brocklesby (1963) were not available for re-examination. Cotylophoron indicum Stiles and Goldberger, 1910; C. madrasense Gupta, 1958 and C. chauhani Gupta and Gupta, 1972, as already discussed under the genus Paramphistomum, are all junior synonyms of Paramphistomum epiclitum Fischoeder, 1901.

According to Mitskevich (1958), Skrjabin (1931) cited Gubornov as to have reported Cotylophoron skrjabini as a new species but no description has been published for the species, therefore the name is not available. Yamaguti (1971) listed the name as nomen nudum. Mitskevich (1958) described C. skrjabini as a new species from

Rangifer tarandus in the U.S.S.R. The writer was unable to obtain the type specimens for re-examination but Velichko (1973) has already shown that the specimens actually consisted of two species, Calicophoron calicophorum and Liorchis scotiae (= Paramphistomum leydeni). Mitskevich's only figure for the species strongly suggests close similarity to P. leydeni.

Price and McIntosh (1953) described C. noveboracensis as a new species from sheep in the United States. They claimed that although it is closely related to C. fuelleborni, it is smaller and has a different geographical distribution. Re-examination of the type specimens of both species (C. fuelleborni loaned from the Zoologisches Museum an der Alexander von Homboldt Universität zu Berlin, Coll. No. 6446 and C. noveboracensis loaned from the United States National Parasite Collection, USDA, Beltsville, Maryland, USNMH Coll. No. 48744 & 4596) has revealed no distinct morphological difference between the two species. They are here considered synonymous, C. fuelleborni has priority over C. noveborancensis.

The type specimens of C. guangdongense Wang, 1979 could not be obtained for re-examination. It was separated however from closely related species based on minor differences of characters which are considered here variable. The species therefore is regarded here as a junior synonym of C. cotylophorum. Although the type specimens of C. xiangjiangense Wang, 1979 was also unobtainable for re-examination in this study, it was described however to possess a pharynx of the liorchis type and an acetabulum of the paramphistomum type. Because of these, it differs from the rest of the species in genus.

Cotylophoron ottoi Gupta and Bakhshi in Gupta and Nakhasi, 1977 was described briefly from Bos indicus and Bubalus bubalis in India. It was not differentiated from the rest of the species in the genus. The terminal genitalium was referred to the cotylophoron type, i.e. surrounded by a genital sucker but their illustration of this structure (Fig. 1) does not seem to indicate the presence of a sucker. A footnote was added stating that the species is under publication but as to date, no further description has appeared in literature. The discrepancy can only be verified by examination of the type specimens but their deposition is not indicated in the paper and efforts to obtain the types and other specimens from the authors have failed despite several requests. From the available description and insufficient illustration of the species, its is very difficult to ascertain its status and until the types and further materials are available for examination, the species is here regarded as species inquirenda.

Only seven species of Cotylophoron are here considered valid namely, Cotylophoron cotylophorum (Fischoeder, 1901) Stiles and Goldberger, 1910; C. jacksoni Näsmark, 1937; C. fuelleborni Näsmark, 1937; C. panamensis Price and McIntosh, 1953; C. bareilliensis Mukherjee and Chauhan, 1965; C. macrosphinctris Sey and Graber, 1979 and C. xiangjiangense Wang, 1979 and they are separable by a key given below.

Key to the species of the genus Cotylophoron Stiles and Goldberger, 1910

1. Pharynx of the liorchis type; acetabulum of the paramphistomum type - - - - - - - - - - - *C. xiangjiangense*

   Pharynx of the calicophoron type; acetabulum of the cotylophoron type - - - - - - - - - - - - - - - - - - - 2

2. Oesophageal bulb present - - - - - - - - - - - - - - - - - - - 3

   Oesophageal bulb absent - - - - - - - - - - - - - - - - - - - 4

3. Genital sucker with a sphincter (schistocotyle type); genital papilla broad and cylindrical - - - - - *C. macrosphinctris*

   Genital sucker without a sphincter (cotylophoron type); genital papilla slender and tapers towards its free end - - - - - - - - - - - - - - - - - - *C. cotylophorum*

4. Vitellaria confluent dorso-medially in their posterior limit; testes usually juxtaposed - - - - - - - - - *C. panamensis*

   Vitellaria not confluent dorso-medially; testes directly or obliquely tandem - - - - - - - - - - - - - - 5

5. Testes smaller than ovary - - - - - - - - - - *C. bareilliense*

   Testes larger than ovary - - - - - - - - - - - - - - - - - - - 6

6. Wall musculature of oesophagus very thick - - - - - *C. jacksoni*

   Wall musculature of oesophagus thin - - - - - - *C. fuelleborni*

Revision of the genus Orthocoelium (Stiles and Goldberger, 1910) Price and McIntosh, 1953

INTRODUCTION

When Fischoeder (1901. 1902, 1903) described Paramphistomum orthocoelium, P. dicranocoelium and P. streptocoelium, he placed them in a separate group (section B) because Laurer's canal does not cross the excretory vesicle in these species. A year later (1904), he described another species, P. scoliocoelium which also possesses the above mentioned character. Based on the same character, Stiles and Goldberger (1910) proposed Orthocoelium as a subgenus under Paramphistomum and assigned to it P. orthocoelium and P. dicranocoelium with the former as the type species, and they stated that eventually, this subgenus will be recognised as a distinct genus. They assigned P. streptocoelium and P. scoliocoelium and two other new species, P. shipleyi and P. parvipapillatum which are also characterized by Laurer's canal not crossing the excretory vesicle or duct to an uncertain subgenus.

Of the above mentioned species, only P. orthocoelium was recognised as valid by Maplestone (1923) and the others as its synonyms. This synonymy was followed by Fukui (1929) and Travassos (1934) but Näsmark (1937), after re-examination of Fischoeder's materials and making sections of them, confirmed the validity of Fischoeder's species. He erected the genus Ceylonocotyle for their reception, but without type designation, because Laurer's canal does not cross the excretory vesicle or duct. He regarded P. shipleyi as a synonym of Ceylonocotyle scoliocoelium (Fischoeder,

1904) and P. parvipapillatum as a synonym of either C. scoliocoelium (Fischoeder, 1904) or C. dicranocoelium (Fischoeder, 1901).

Skrjabin (1949) accepted the genus Ceylonocotyle but Price and McIntosh (1953) pointed out that the subgenus Orthocoelium Stiles and Goldberger, 1910 has priority over Ceylonocotyle Näsmark, 1937 because under the rules of the International Code for Zoological Nomenclature, subgenera have the same nomenclatural status as genera. They also tentatively moved Cotylophoron okapi Leiper, 1935 to Orthocoelium in a new combination. Recently however, Eduardo (1980c) erected the genus Leiperocotyle to contain C. okapi because of the presence of a genital sucker and that Laurer's canal does not cross the excretory vesicle or duct. Yamaguti (1958) and Mukherjee and Chauhan (1965), although aware of Price and McIntosh's paper (1953), accepted Ceylonocotyle without giving any reason. The latter authors also moved Paramphistomum cuonum Bhalerao, 1937; P. maplestonei Bhalerao, 1937 and P. spinicephalus Tandon, 1955 to the genus Ceylonocotyle in new combinations. Earlier, Yamaguti (1958) erected the genera Pseudoparamphistoma and Paramphistomoides to contain P. cuonum and P. maplestonei respectively and later (1971) he maintained the same generic arrangement of the two species but listed P. spinecephalus Tandon, 1955 under the genus Paramphistomum with a note "generic status sub judice". Several species have been subsequently described under Ceylonocotyle namely, Ceylonocotyle dawesi Gupta, 1958 from domestic ruminants in India; C. petrovi Davydova, 1961 from Cervus nippon in Russia; C. naesmarki Mukherjee, 1963 from sheep in India; C. gigantopharynx Schad, Kuntz, Anteson and Webster, 1964 (a new name proposed for Paramphistomum gotoi of

Dawes, 1936 and of Tandon, 1955b but not of Fukui, 1922) and C. scoliocoelium var. benoiti Gretillat, 1966 from Syncerus caffer in Central Africa. Velichko (1966) after re-examining the type specimens of C. petrovi Davydova, 1961 came to the conclusion that the species belongs to the genus Paramphistomum and moved it to that genus in a new combination. Yamaguti (1971) realised the validity of Orthocoelium ovar Ceylonocotyle and listed all species previously assigned to the latter under the former genus. However, without giving any reason, he listed Ceylonocotyle gigantopharynx Schad, Kuntz, Anteson and Webster, 1964 under the genus Paramphistomum. Two species were lately described under Ceylonocotyle, C. narayanai Gupta and Gupta, 1972 and C. tamilensis Gupta and Bakhshi in Gupta and Nakhasi, 1977 but Eduardo (1980b) has now moved both species to Orthocoelium in new combinations. He also described a new species, Orthocoelium indonesiense from ruminants in Indonesia. In another paper, the same author (1980c) synonymized Cochinocotyle Gupta and Gupta, 1970 with Orthocoelium and moved its only species, C. bovini to the latter genus in a new combination.

In this study, only eleven species including one new are considered valid under the genus Orthocoelium. They are here described and illustrated and their synonymies discussed.

SYNONYMS: Ceylonocotyle Näsmark, 1937

Cochinocotyle Gupta and Gupta, 1970

GENERIC DIAGNOSIS

Paramphistomidae, Orthocoeliinae. Body conical, almost round in cross section, small to medium in size; ventral pouch absent. Acetabulum small, subterminal or terminal. Pharynx without pouch or diverticle; oesophagus with or without posterior sphincter or bulb; caeca in lateral sides of the body, straight or wavy. Testes unlobed or lobed, directly or obliquely tandem; seminal vesicle thin-walled and coiled; pars musculosa well developed and convoluted; pars prostatica short or long; cirrus pouch absent. Ovary and Mehlis' gland posttesticular; uterus winds forward, dorsal to the testes then ventral to the male ducts; vitellaria in lateral fields; Laurer's canal does not cross the excretory vesicle or duct. Genital sucker absent. Parasitic in the stomach of ruminants.

Type species: Orthocoelium orthocoelium (Fischoeder, 1901)
Price and McIntosh, 1953

Orthocoelium orthocoelium (Fischoeder, 1901) Price and McIntosh, 1953

Synonym: Paramphistomum spinicephalus Tandon, 1955

TYPE SPECIMENS: United States National Parasite Collection, USDA, Beltsville, Maryland (USNMH Coll. No. 3373, co-types)

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Bubalus bubalis	Bangladesh	British Museum (Natural History) coll. no. 1969. 2.25.62-63, labeled "P. epiclitum".
	Sri Lanka	Naturhistoriska riksmuseet (Stockholm), Näsmark's material.
	Philippines	Author's own collection
Cattle	Shanghai, China	London School of Hygiene & Tropical Medicine
	Malaysia	Dr. Siew Kein Lee
	?	British Museum (Natural History) coll. no. 1962. 11.7.1201-1249.
Swamp deer	India	British Museum (Natural History) coll. no. 1965. 4.2.56-70, 71-85.

HABITAT: Rumen and reticulum

DESCRIPTION:

Body conical and nearly straight, 5.80-8.21 mm long, 1.80-3.52 mm in the dorso-ventral direction. Body surface has papillae on the anterior end around the oral opening.

Acetabulum subterminal, 1.00-1.47 mm in external diameter in the dorso-ventral direction; ratio to body length 1:4.9 to 1:6.5; of the streptocoelium type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 25-33; d.i.c., 27-43; v.e.c., 23-38; v.i.c., 32-45; m.e.c., 3-7.

Pharynx 0.90-1.45 mm long, 0.70-1.12 mm in the dorso-ventral direction; ratio to body length 1:5.5 to 1:7.8, to the diameter of the acetabulum 1:1 to 1:1.2; of the orthocoelium type (new type) in median sagittal section; characterized by the presence of a group of ciruclar muscle units near the anterior end forming an anterior sphincter, the exterior and middle circular series joined together in their anterior and posterior ends, interior circular and longitudinal fibres present, radial fibres well developed. Oesophagus long and broad (1.40-1.47 by 0.42-0.78 mm), musculature of wall relatively thin but thickened in its posterior end to form a small sphincter, lumen lined by thick hyaline layer thrown into folds. Caeca in lateral sides of the body, broad, straight in their course, reach level of acetabulum or just short of it.

Testes relatively small, lobed, usually kidney-shaped, tandem in posterior half of the body; anterior testis 0.45-0.62 mm long, 0.85-1.23 mm in the dorso-ventral direction; posterior testis 0.56-0.60 mm long, 0.82-0.98 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa relatively well developed, thick-walled and convoluted; pars prostatica relatively small, 0.21-0.38 by 0.14-0.25 mm.

Ovary subspherical, 0.20-0.35 by 0.25-0.38 mm, posterior to testes and anterior to acetabulum; Mehlis' gland close to ovary, 0.21-0.29 by 0.20-0.26 mm; uterus winds forward, dorsal to the testes then ventral to the male ducts; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface about 1.86-2.30 mm anteriorly to the excretory pore; vitellaria in lateral fields, consist of groups of small follicle, extend from level of middle of oesophagus to anterior level of acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 100-115 by 60-65 µm.

Genital pore opens on the ventral surface at a level about the middle of the oesophagus; terminal genitalium of the ortho-coelium type (new type) in median sagittal section characterized by the large size, thick genital papilla and presence of a well developed genital sphincter and sphincter papilla.

Excretory vesicle dorsal to acetabulum; excretory pore opens on the dorsal surface posteriorly to the Laurer's canal opening.

FIGURE 137

Orthocoelium orthocoelium (Fischoeder, 1901)

Price and McIntosh, 1953

a. Whole worm, ventral view

b. Whole worm, sagittal view

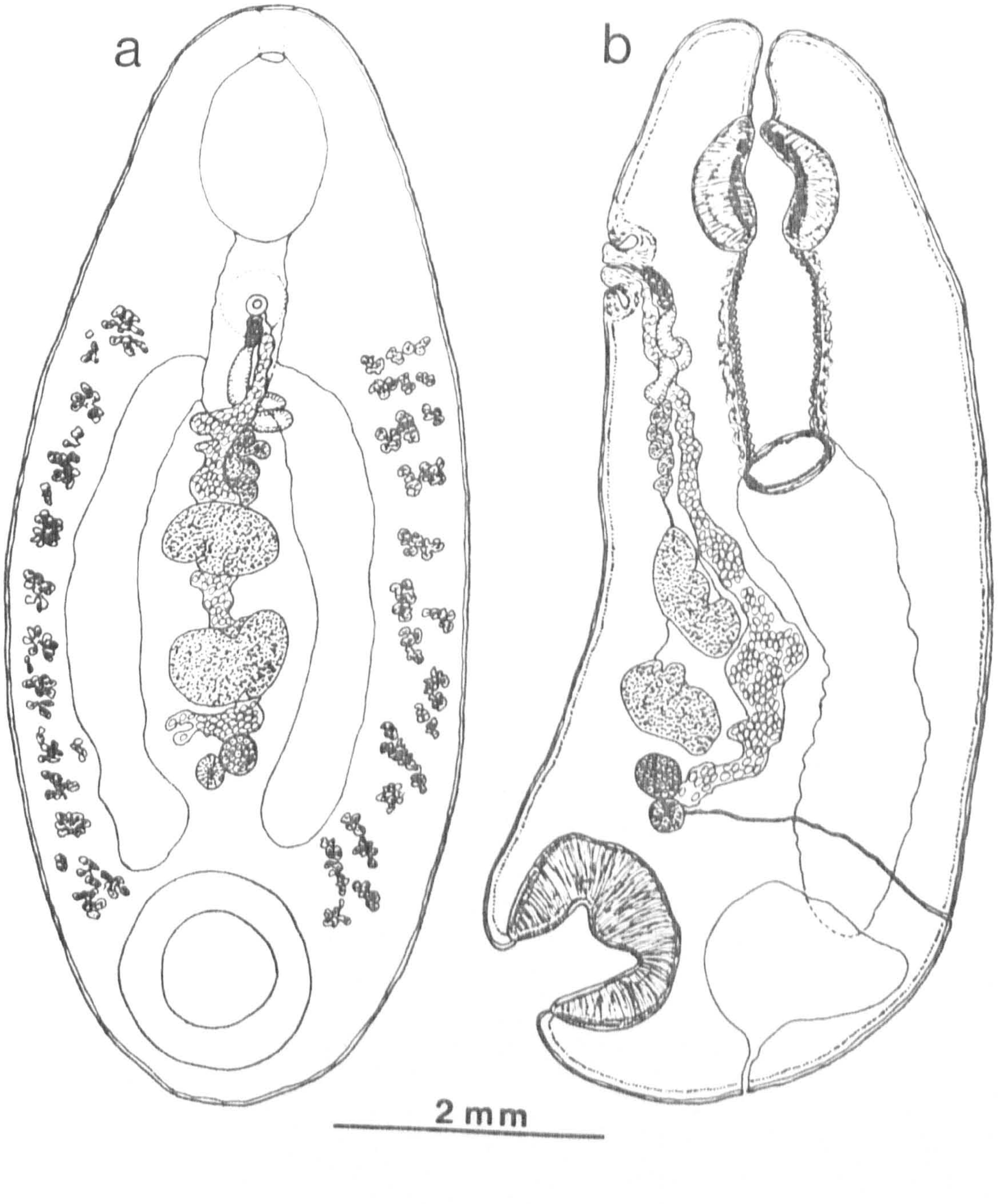

a
b
2 mm

FIGURE 138

Orthocoelium orthocoelium (Fischoeder, 1901)

Price and McIntosh, 1953

(median sagittal section)

a. Acetabulum (streptocoelium type)

b. Pharynx (orthocoelium type) and oesophagus, note lining thrown into folds and the presence of a posterior sphincter.

c. Terminal genitalium (orthocoelium type) and pars prostatica

a

0.5 mm

b

0.5 mm

C

0.3 mm

Orthocoelium streptocoelium (Fischoeder, 1901) Yamaguti, 1971

TYPE SPECIMENS: United States National Parasite Collection, USDA, Beltsville, Maryland (USNMH Coll. No. 3374, co-types), from the rumen of Bos kerabau in Ceylon (now Sri Lanka).

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collection

Bubalus bubalis	Malaysia	Dr. Kein Siew Lee
	Sri Lanka	Naturhistoriska riksmuseet (Stockholm), Näsmark's material.

HABITAT: Rumen

DESCRIPTION:

Body conical, nearly straight, 5.00-9.21 mm long, 1.32-2.50 mm in greatest width in the dorsao-ventral direction.

Acetabulum subterminal, 0.89-1.41 mm in external diameter in the dorso-ventral direction; ratio to body length 1:6.5 to 1:8; of the streptocoelium type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 19-23; d.i.c., 25-30; v.e.c., 18-23; v.i.c., 23-27; m.e.c., 7-10.

Pharynx 0.44-1.00 mm long, 0.55-0.75 mm in the dorso-ventral direction; ratio to body length 1:2 to 1:2.5; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section. Oesophagus 0.52-1.00 mm long, musculature of wall moderate in thickness, posterior end thickened to form a posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides, form shallow dorso-ventral bends, reach level of acetabulum with the blind ends directed ventrally.

Testes lobed, tandem in posterior half of the body; anterior testis 0.60-0.92 mm long, 0.84-0.88 mm in the dorso-ventral direction; posterior testis 0.30-0.61 mm long, 0.52-0.83 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa well developed, thick-walled and convoluted; pars prostatica 0.31-0.90 mm long and 0.20-0.24 mm wide.

Ovary subspherical, 0.26-0.43 by 0.30-0.60 mm, posterior to testes and anterior to acetabulum; Mehlis' gland close to ovary, 0.21-0.22 by 0.30-0.34 mm; uterus winds forward, dorsal to the testes then ventral to the male ducts; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface about 0.50-0.65 mm anteriorly to the excretory pore; vitellaria in lateral fields, extend from level of oesophagus to acetabulum, not confluent dorso-medially in their anterior or postrior limits; egg 105-115 by 60-65 µm.

Genital pore opens on the ventral surface at a level posterior to the oesophageal bifurcation; terminal genitalium of the streptocoelium type (sensu Näsmark, 1937) in median sagittal section, easily distinguished by the sphincter papilla which is extensive and connected to the well developed genital sphincter.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface posteriorly to the Laurer's canal opening.

FIGURE 139

Orthocoelium streptocoelium (Fischoeder, 1901) Yamaguti, 1971

Whole worm, sagittal view

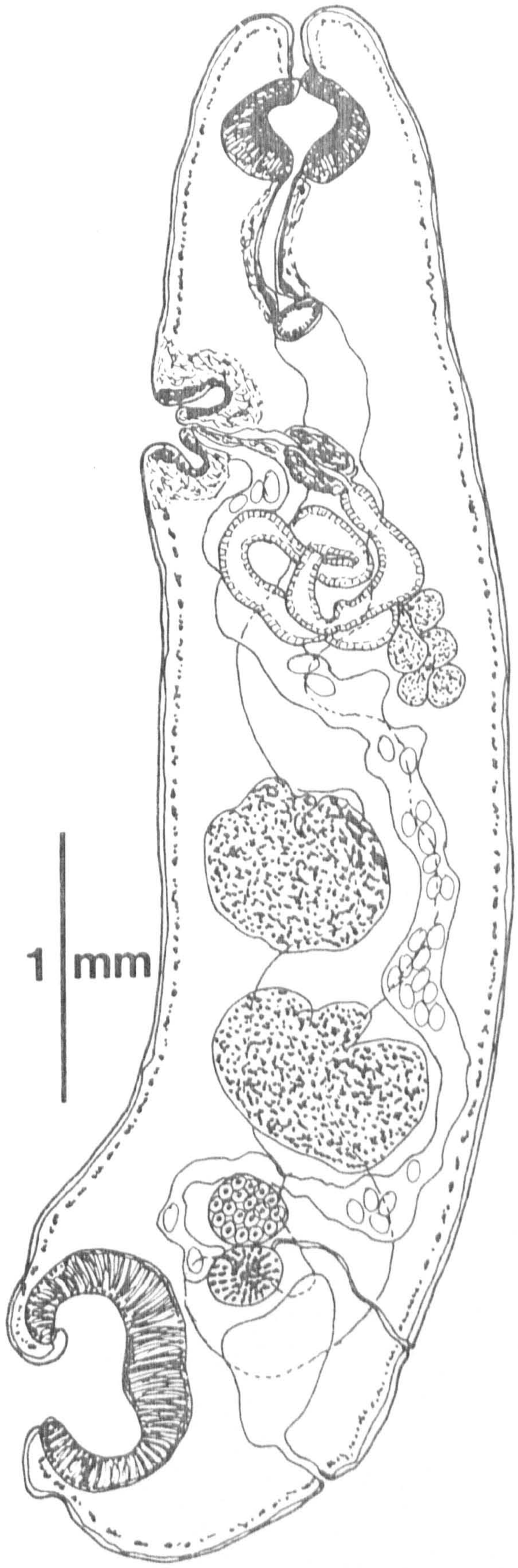

1 mm

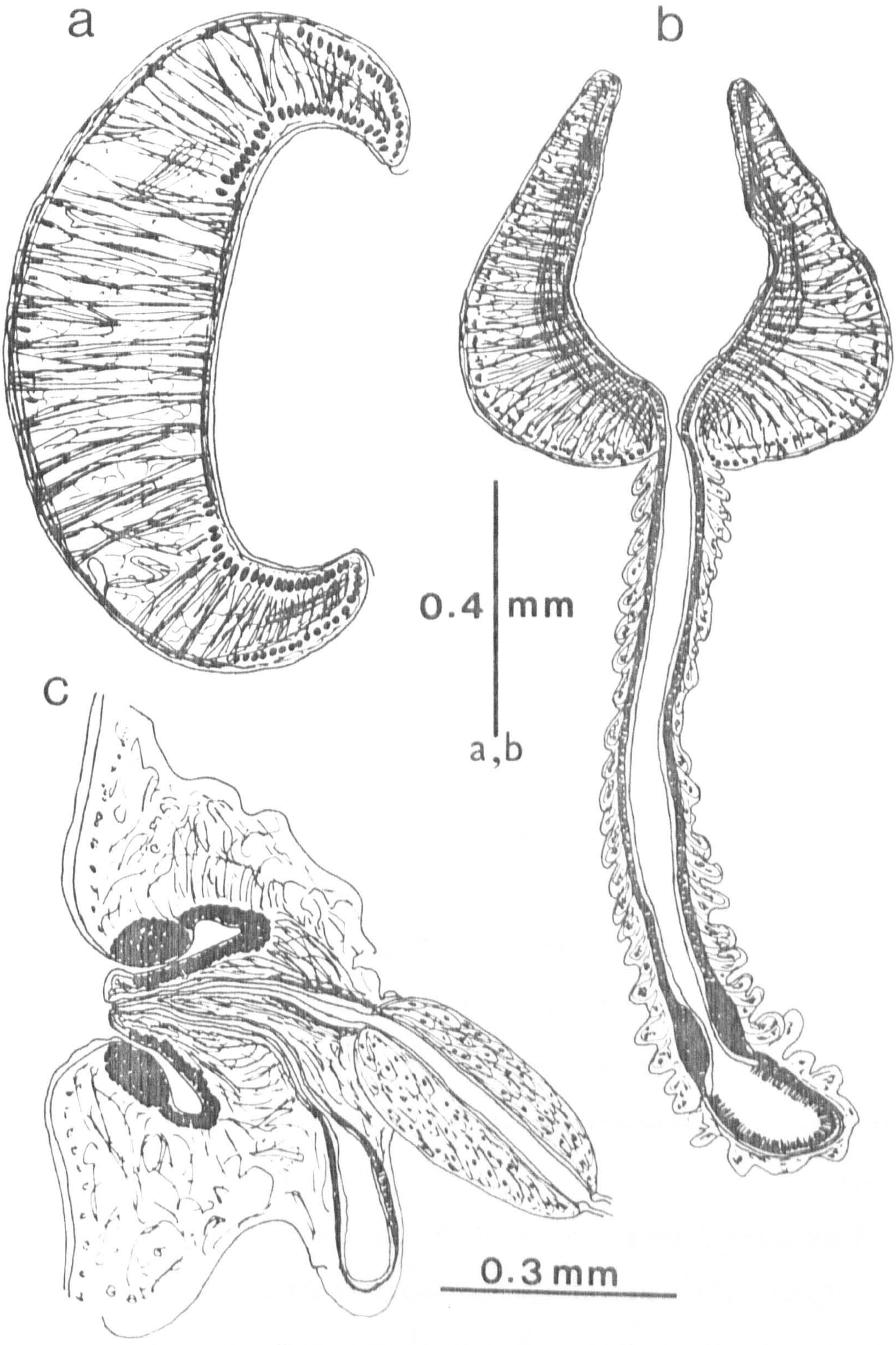
FIGURE 140

Orthocoelium streptocoelium (Fischoeder, 1901) Yamaguti, 1971
(median sagittal section)

a. Acetabulum (streptocoelium type)

b. Pharynx (calicophoron type) and oesophagus, note presence of a sphincter in the posterior end of oesophagus.

c. Terminal genitalium (streptocoelium type) and pars prostatica


a
b
C
0.4 mm
a,b
0.3 mm

Orthocoelium dicranocoelium (Fischoeder, 1901) Yamaguti, 1971

Synonym: Ceylonocotyle tamilensis Gupta and Bakhshi in Gupta and Nakhasi, 1977

TYPE SPECIMENS: United States National Parasite Collection, USDA, Beltsville, Maryland (USNMH Coll. No. 3581, co-types), from Bos taurus indicus.

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos taurus	Philippines	Author's own collection
	Sri Lanka	Naturhistoriska riksmuseet (Stockholm), Näsmark's material.
Goat	India	British Museum (Natural History) coll. no. 1967. 3.15.1-20, labeled "P. epiclitum".
Sheep	Indonesia	Mr. M.D. Brotowidjoyo

HABITAT: Rumen

DESCRIPTION:

Body conical, elongate and nearly straight, 4.80-7.23 mm long, 1.30-2.33 mm in greates width in the dorso-ventral direction. Body surface has tegumental papillae on the anterior end around the oral opening and on the posterior end around the acetabular opening. Those on the former are short, stumpy and covered with hair-like processes while those on the latter are dome-shaped, much smaller, fewer and randomly arranged.

Acetabulum subterminal, 0.72-1.16 mm in external diameter in the dorso-ventral direction; ratio to body length 1:6 to 1:6.7; of the streptocoelium type (sensu Näsmark, 1937) in median sagittal

section; number of circular muscle units, d.e.c., 14-18; d.i.c., 23-28; v.e.c., 15-19; v.i.c., 22-26; m.e.c., 7-14.

Pharynx 0.48-0.86 mm long, 0.31-0.49 mm in the dorso-ventral direction; ratio to body length 1:8.3 to 1:9.9, to the diameter of the acetabulum 1:1.2 to 1:1.5; of the dicranocoelium type (sensu Näsmark, 1937) in median sagittal section characterized by the presence of a lip sphincter. Oesophagus 0.46-1.15 mm long, sometimes bend dorsally; musculature of wall thickened in its posterior part into a strong muscular bulb; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, nearly straight in their course, reach level of posterior border of posterior testis or may reach anterior border of acetabulum, blind ends directed posteriorly.

Testes unlobed or just slightly indented, tandem in posterior half of the body; anterior testis 0.94-1.23 mm long, 0.75-1.09 mm in the dorso-ventral direction; posterior testis 1.01-1.32 mm long, 0.78-1.08 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa thick-walled, relatively well developed and convoluted; pars prostatica 0.23-0.52 mm long and 0.17-0.22 mm wide.

Ovary subspherical, 0.31-0.37 by 0.30-0.45 mm, posterior to testes and anterior to acetabulum; Mehlis' gland close to ovary, 0.18-0.26 by 0.26-0.33 mm; uterus winds forward, dorsal to the testes then ventral to the male ducts; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface about 0.50-0.62 mm anteriorly to the excretory pore; vitellaria in lateral fields, extend from level of oesophagus to acetabulum, not

confluent dorso-medially in their anterior or posterior limits; egg 112-138 by 82-90 μm.

Genital pore opens on the ventral surface at a level posterior to the oesophageal bifurcation; terminal genitalium of the gracile type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface posteriorly to the Laurer's canal opening.

FIGURE 141

Orthocoelium dicranocoelium (Fischoeder, 1901) Yamaguti, 1971

(SEM)

a. Whole worm, ventral view (scale bar = 300 µm)

b. Acetabular region (scale bar = 150 µm)

c. Anterior end, note presence of papillae
(scale bar = 100 µm)

d. Genital pore region (scale bar = 100 µm)

e. Closer view of papillae on anterior end, note stumpy shape and surface covered with hair-like processes
(scale bar = 3 µm)

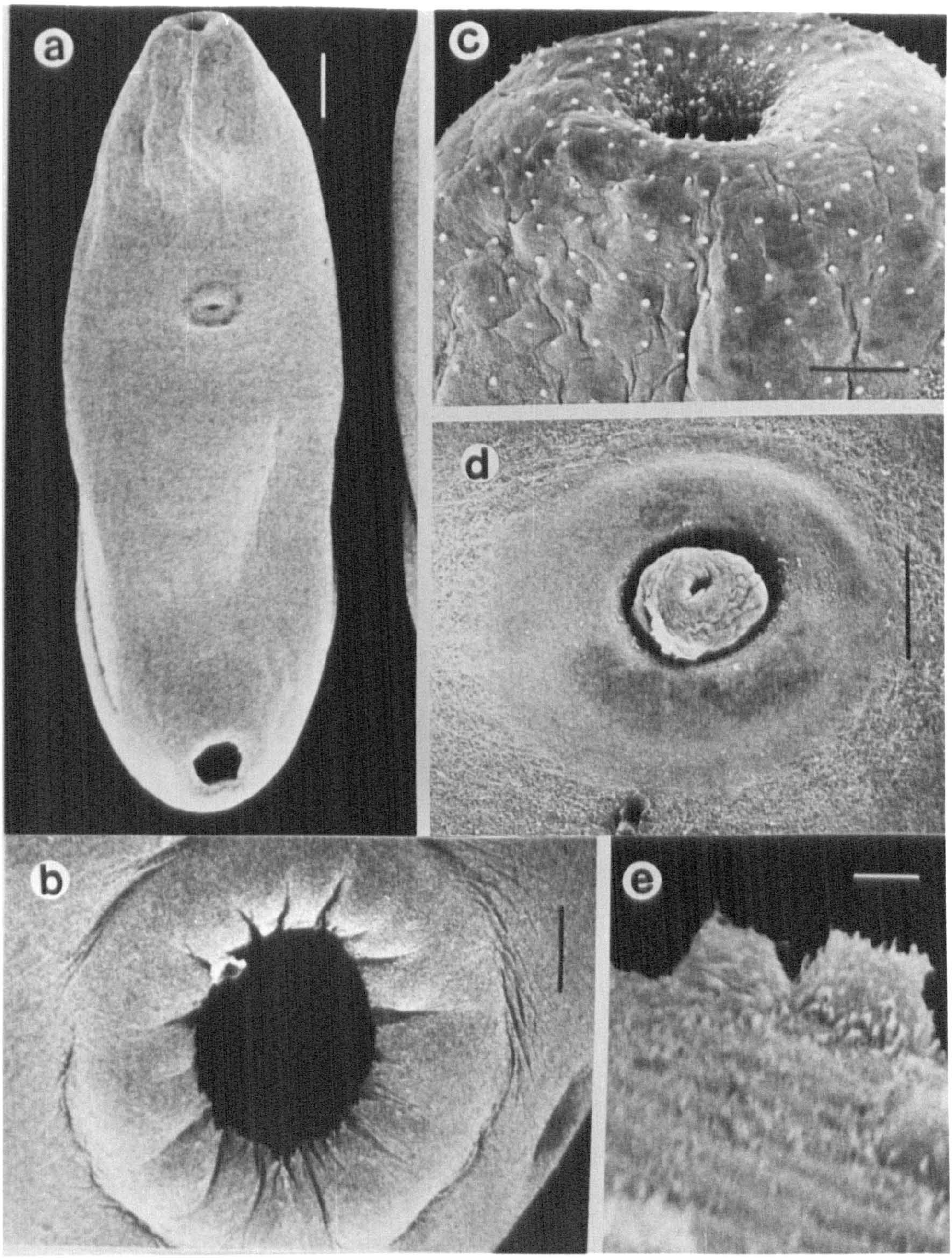

a
c
d
b
e

FIGURE 142

Orthocoelium dicranocoelium (Fischoeder, 1901) Yamaguti, 1971

a. Whole worm, ventral view

b. Whole worm, sagittal view

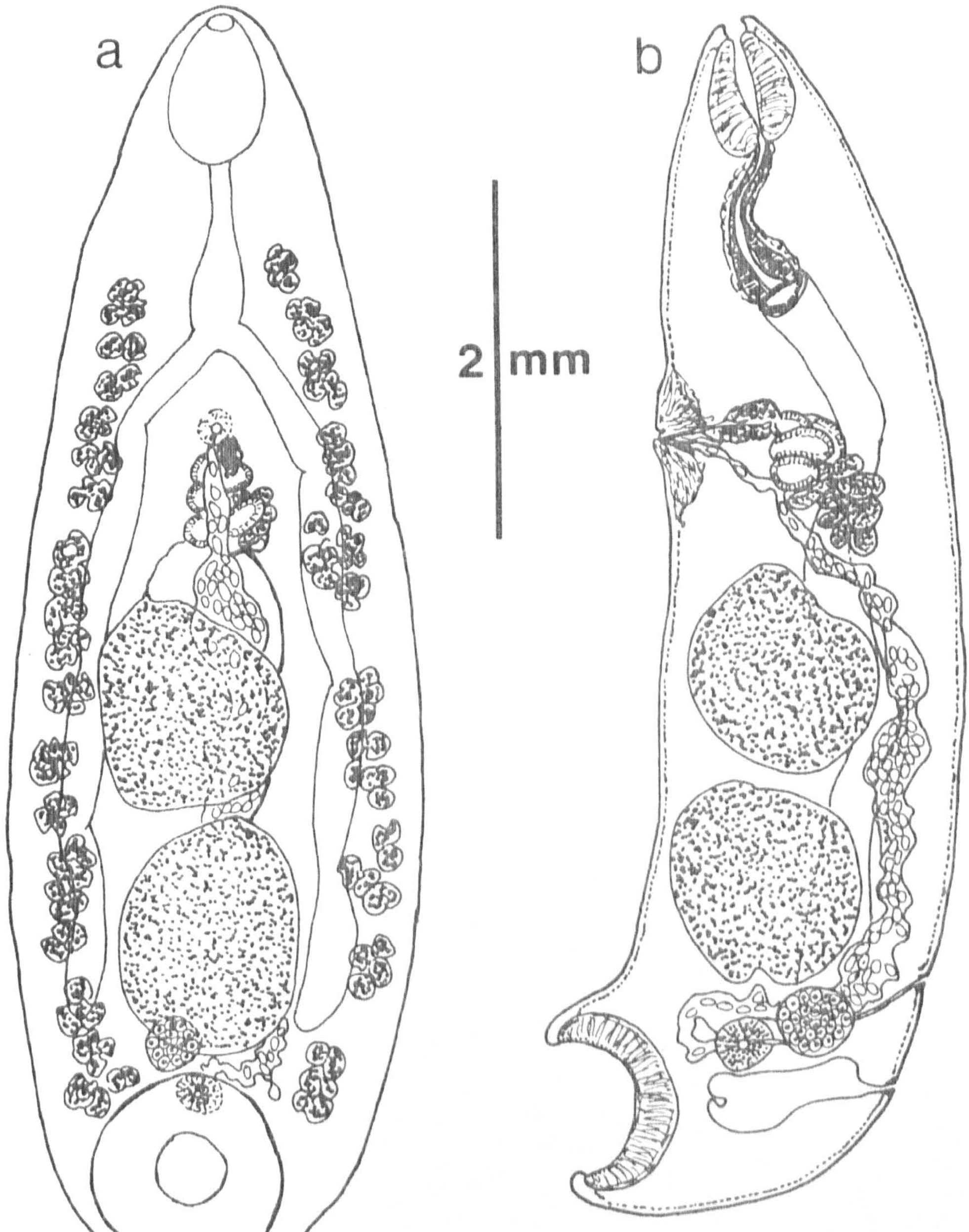

a
b
2 mm

FIGURE 143

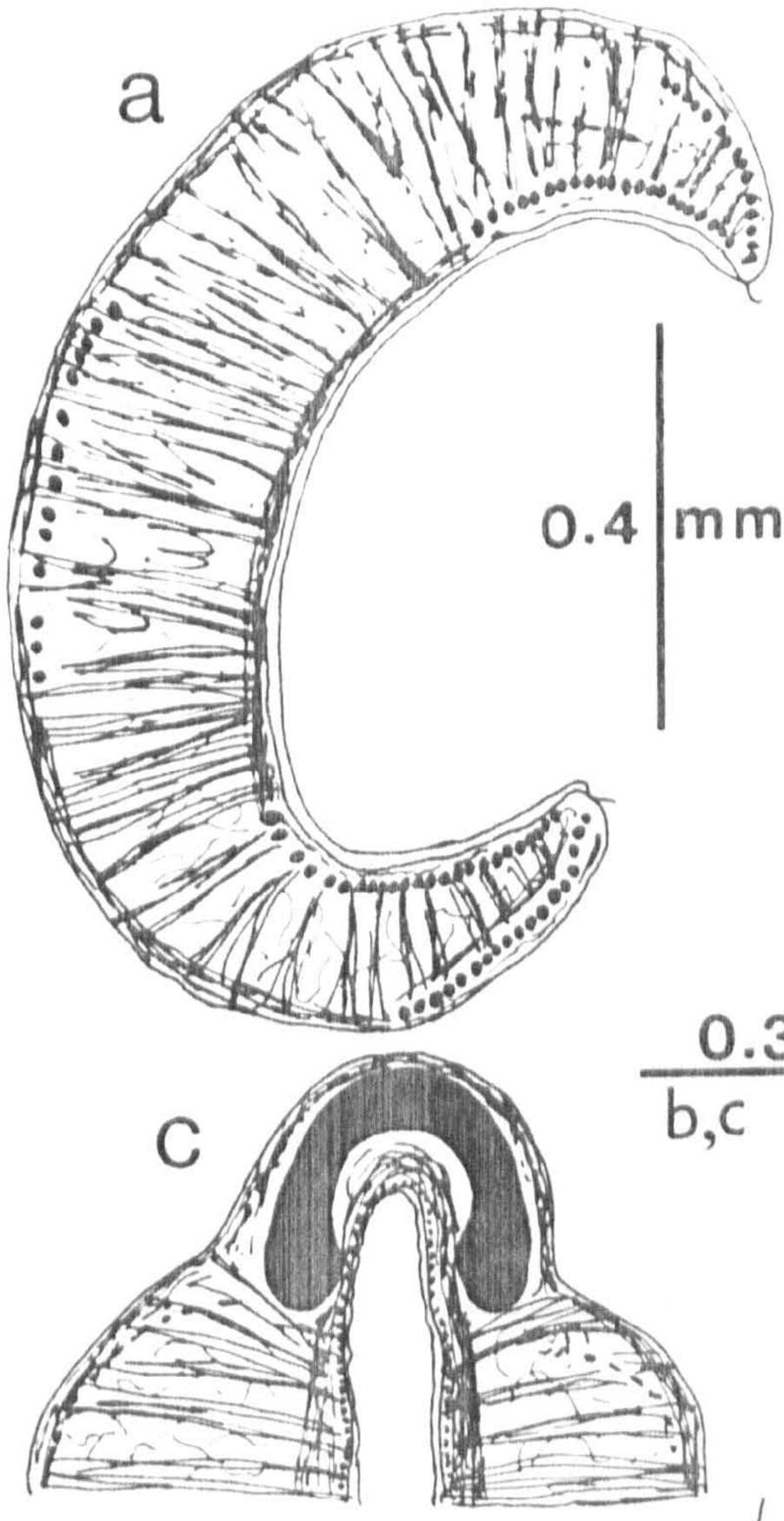
Orthocoelium dicranocoelium (Fischoeder, 1901) Yamaguti, 1971
(sagittal section)

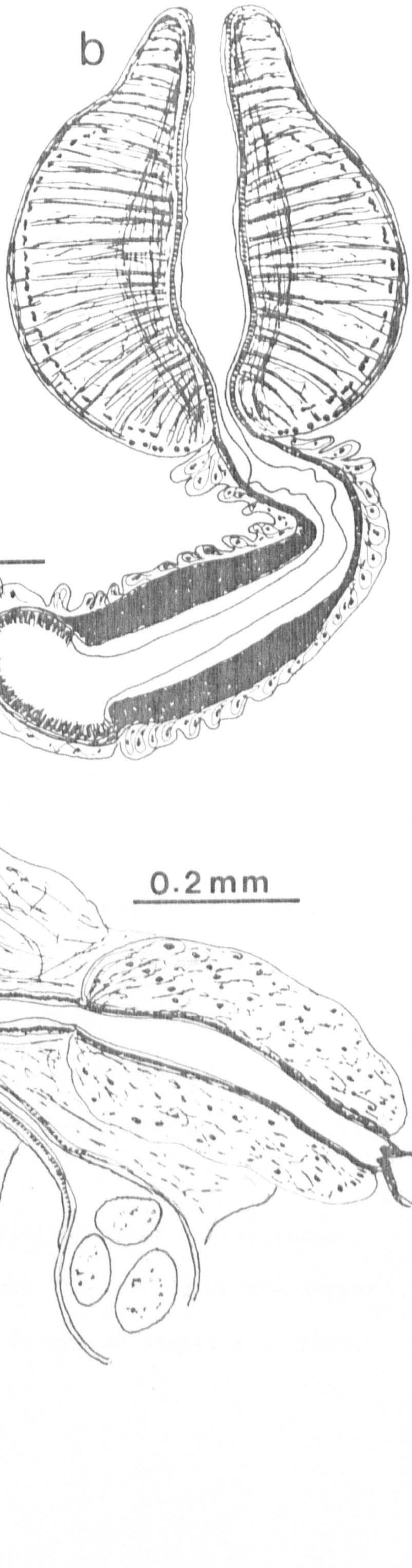
a. Acetabulum (streptocoelium type) median section.

b. Pharynx (dicranocoelium type) and oesophagus, median section. Note that the lip sphincter is not seen in median sagittal section, only in a more lateral section as in c.

c. Pharynx (anterior part) in a more lateral section showing the presence of a lip sphincter.

d. Terminal genitalium (gracile type) and pars prostatica, median section.


a
0.4 mm


b
0.3 mm
b,c

C

0.2 mm
d

Orthocoelium scoliocoelium (Fischoeder, 1904) Yamaguti, 1971

Synonyms: Paramphistomum shipleyi Stiles and Goldberger, 1910
Cotylophoron ovatum Harshey, 1934

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collections

Bos indicus	Chad	Dr. F. Bertin
	Indonesia	Dr. Wardiarto
Bos taurus	Calcutta, India	Naturhistoriska riksmuseet (Stockholm), Näsmark's material.
	Kenya	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
	Philippines	Author's own collection

HABITAT: Rumen and reticulum

DESCRIPTION:

Body small, conical, 2.70-5.22 mm long, 0.87-2.51 mm in greatest width in the dorso-ventral direction. Body surface has tegumental papillae on the anterior end around the oral opening and ventral around the genital pore region and on the posterior end around the acetabular opening. Those around the oral opening are large, conical in shape and densely arranged, those on the genital pore region and around the acetabular opening are much smaller, fewer and randomly arranged.

Acetabulum 0.65-1.11 mm in external diameter in the dorso-ventral direction; ratio to body length 1:3 to 1:6; of the strep-tocoelium type (sensu Näsmark, 1937) in median sagittal section;

number of circular muscle units, d.e.c., 12-18; d.i.c., 20-28; v.e.c., 11-17; v.i.c., 23-30; m.e.c., 10-14.

Pharynx 0.37-0.62 mm long, 0.33-0.48 mm in the dorso-ventral direction; ratio to body length 1:7 to 1:1.0, to the diameter of the acetabulum 1:1.7 to 1:2.3; of the dicranocoelium type (sensu Näsmark, 1937) in median sagittal section. Oesophagus 0.40-0.92 mm long, usually bends dorsally; musculature of wall developed into a strong muscular bulb in its posterior part; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form irregular and shallow dorso-ventral bends, reach level of acetabulum with the blind ends directed postero-ventrally.

Testes realtively large, unlobed or slightly lobed, directly tandem in posterior half of the body; anterior testis 0.60-1.11 mm long, 0.52-1.50 mm in the dorso-ventral direction; posterior testis 0.66-0.92 mm long, 1.33-1.77 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa thick-wall, well developed and convoluted; pars prostatica 0.19-0.35 mm long and 0.09-0.18 mm wide.

Ovary subspherical, 0.20-0.40 by 0.20-0.48 mm, posterior to testes and dorsal to acetabulum; Mehlis' gland close to ovary, 0.13-0.37 by 0.26-0.50 mm; uterus winds forward, dorsal to the testes then ventral to the male ducts; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface about 0.35-0.45 mm anteriorly to the excretory pore; vitellaria in lateral fields, consist of groups of large follicles, extend from level of pharynx to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 120-130 by 70-80 µm.

Genital pore opens on the ventral surface at level of the oesophageal bifurcation or immediately posterior to it; terminal genitalium of the scoliocoelium type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum and posterior to ovary and Mehlis' gland; excretory pore opens on the dorsal surface posteriorly to the Laurer's canal opening.

FIGURE 144

Orthocoelium scoliocoelium (Fischoeder, 1904) Yamaguti, 1971

(SEM)

a. Whole worm, ventral view (scale bar = 300 µm)

b. Anterior end, note presence of large papillae (scale bar = 50 µm)

c. Genital pore region (scale bar = 50 µm)

c. Acetabular region (scale bar = 100 µm)

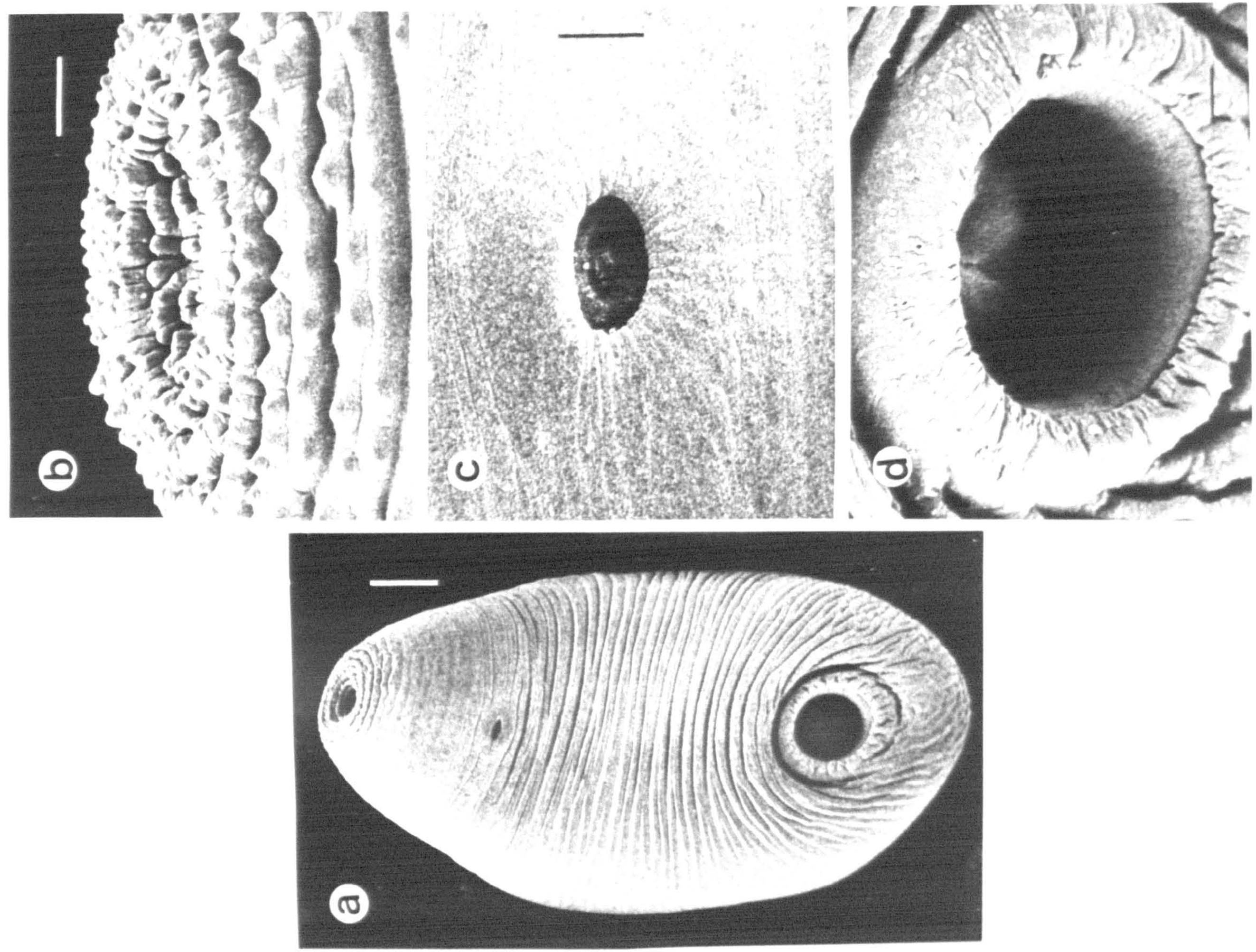

b
c
d
a

FIGURE 145

Orthocoelium scoliocoelium (Fischoeder, 1904) Yamaguti, 1971

a. Whole worm, ventral view

b. Whole worm, sagittal view

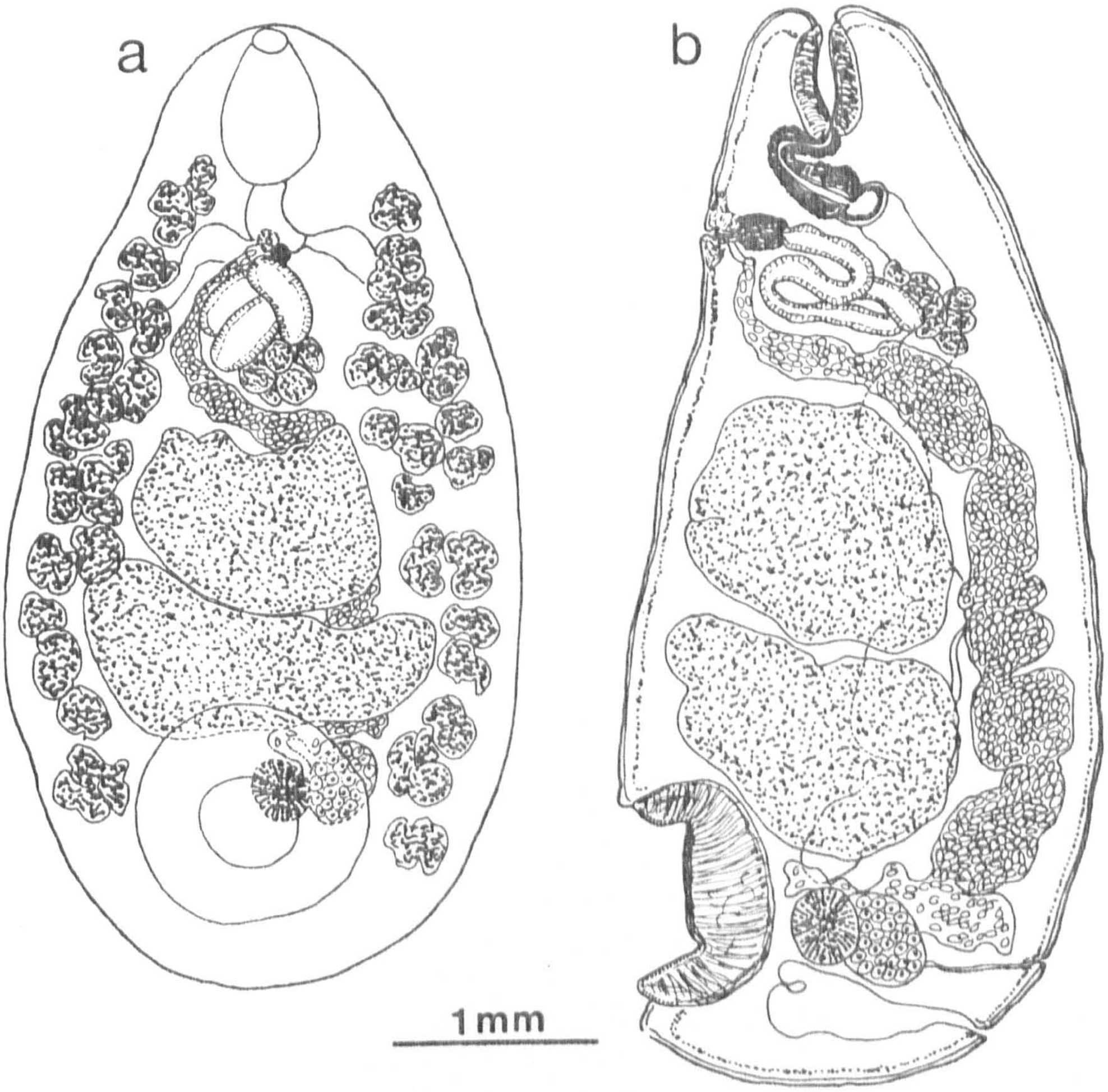

a
b
1mm

FIGURE 146

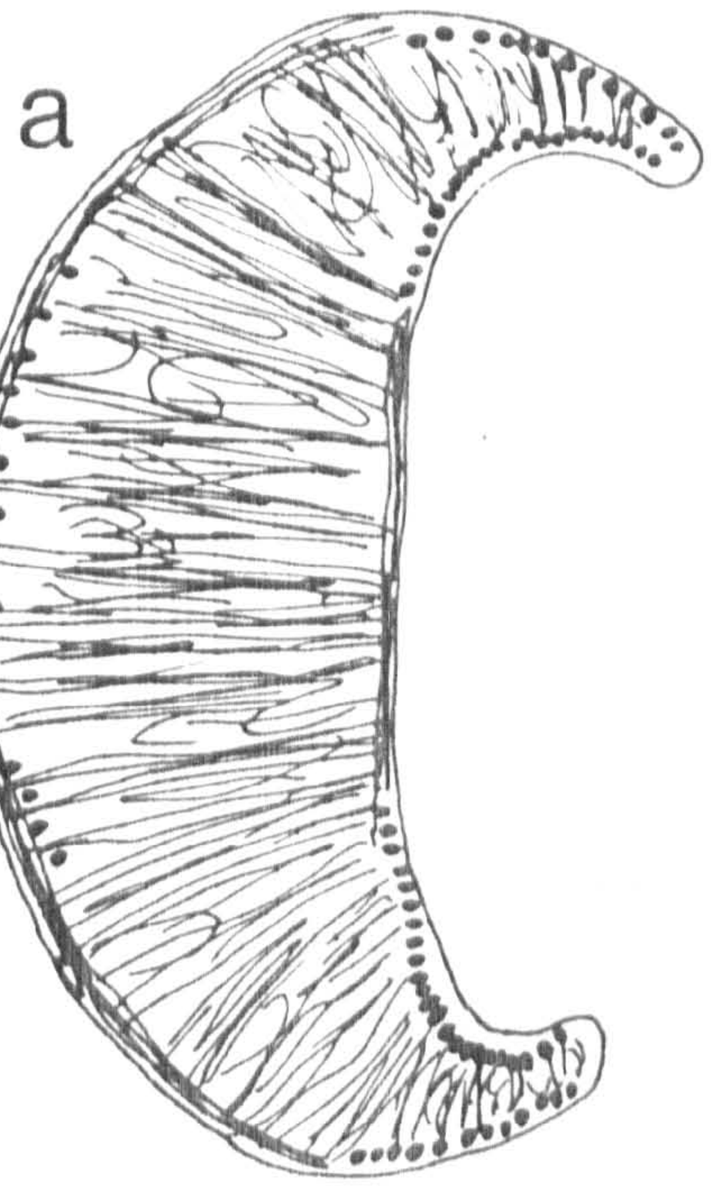
Orthocoelium scoliocoelium (Fischoeder, 1904) Yamaguti, 1971
(sagittal section)

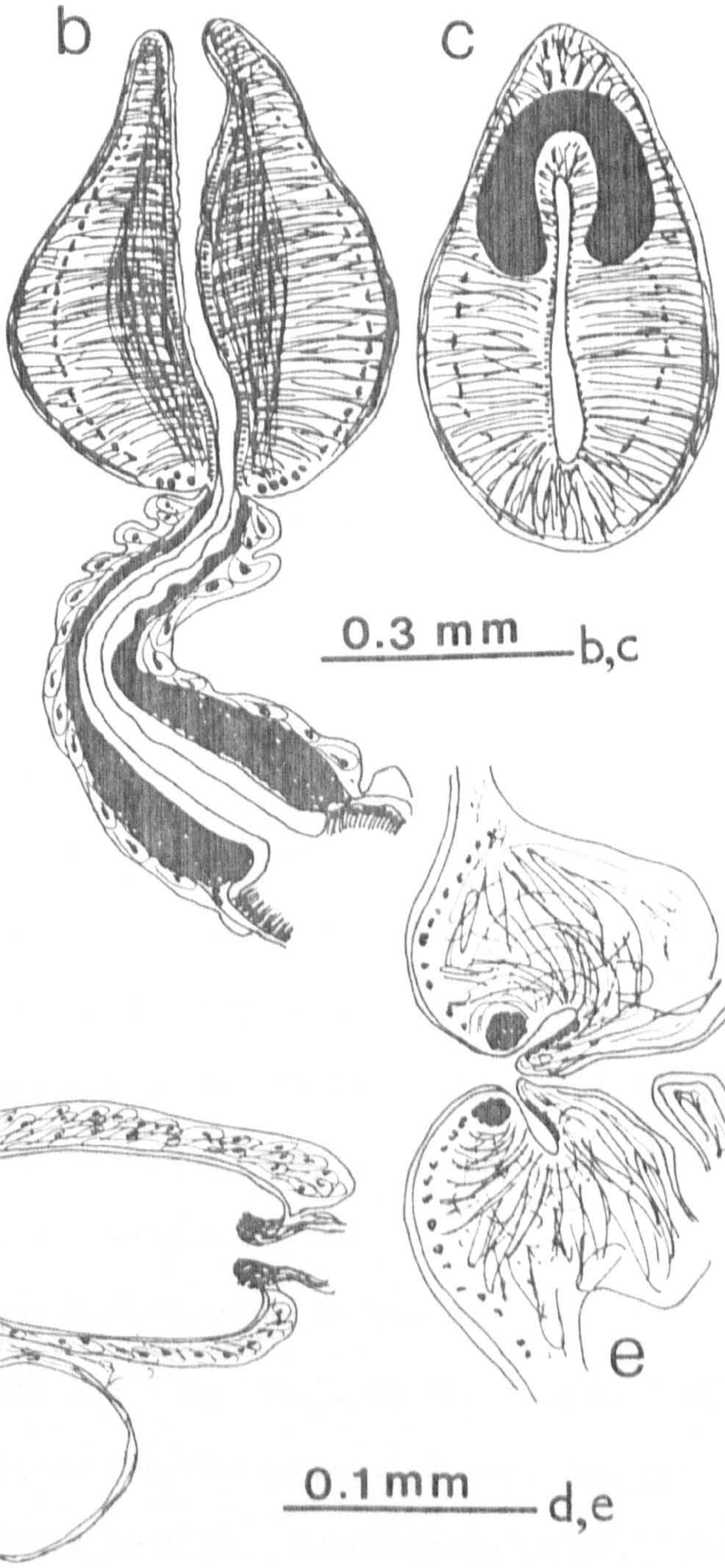
a. Acetabulum (streptocoelium type), median section.

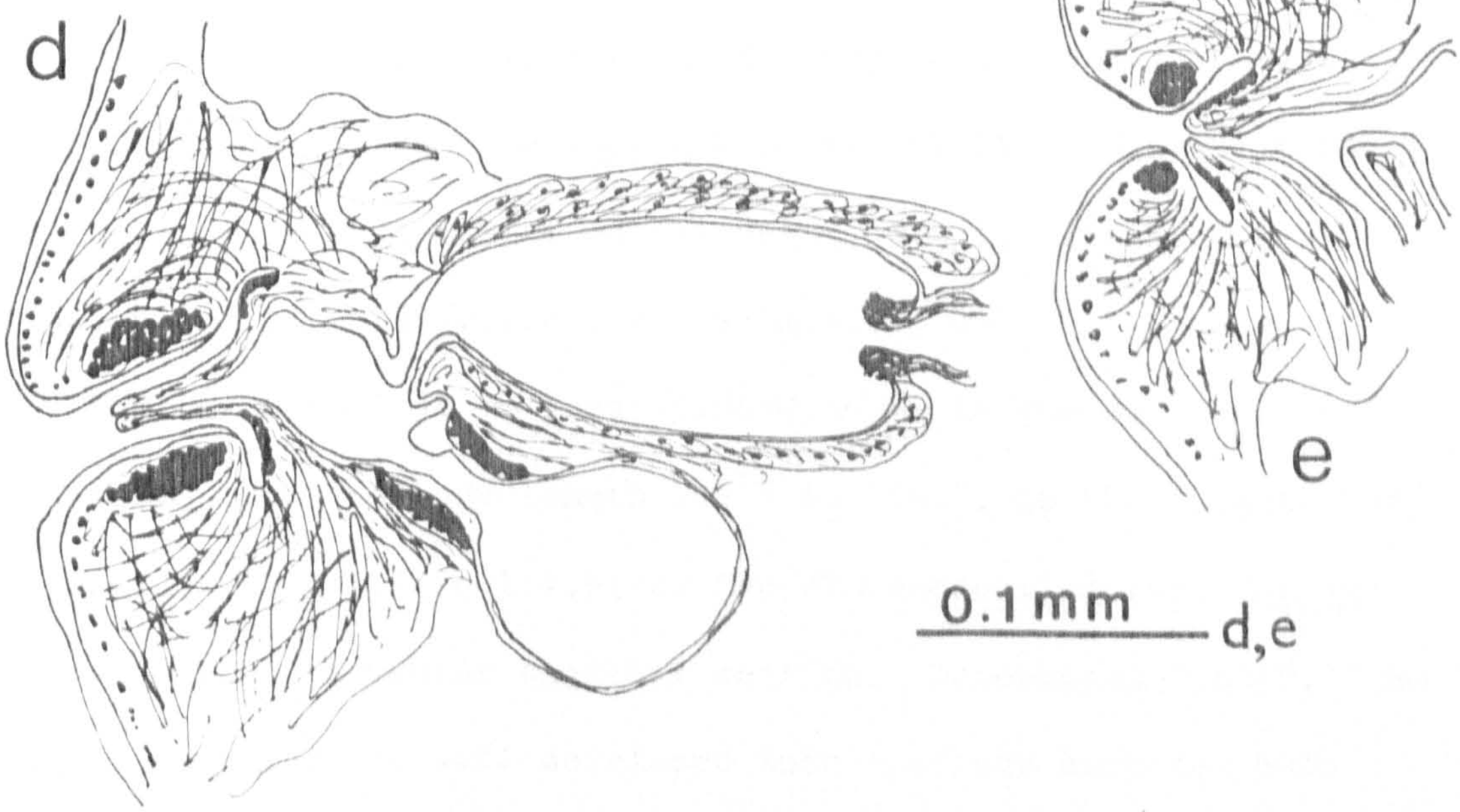
b. Pharynx (dicranocoelium type) and oesophagus, median section. Note that in this particular section the lip sphincter could not be seen.

c. Pharynx in a more lateral section showing the presence of a lip sphincter.

d - e. Terminal genitalium (scoliocoelium type), in d is also shown the pars prostatica.


a
0.3 mm


b
c
0.3 mm
b,c


d
e
0.1 mm
d,e

Orthocoelium parvipapillatum (Stiles and Goldberger, 1910) n. comb.

TYPE SPECIMENS: United States National Parasite Collection, USDA, Beltsville, Maryland (USNMH Coll. No. 9962), from the reticulum of a calf in Pharapatoom, Siam (now Thailand).

OTHER MATERIALS EXAMINED: Hosts, localities and donors/collections

Bubalus bubalis	Punjab, India	Naturhistoriska riksmuseet (Stockholm), Näsmark's material and labeled "Ceylonocotyle scoliocoelium".
Sheep	Indonesia	Mr. M.D. Brotowidjoyo

HABITAT: Rumen and reticulum

DESCRIPTION:

Body small, conical, 2.98-3.90 mm long, 1.00-2.30 mm in greatest width in the dorso-ventral direction.

Acetabulum subterminal, 0.50-0.91 mm in external diameter in the dorso-ventral direction; ratio to body length 1:3.4 to 1:3.7; of the streptocoelium type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 16-19; d.i.c., 23-28; v.e.c., 14-18; v.i.c., 24-29; m.e.c., 3-8.

Pharynx 0.48-0.54 mm long, 0.34-0.36 mm in the dorso-ventral direction; ratio to body length 1:5.5 to 1:6.7, to the diameter of the acetabulum 1:1.8 to 1:1.6; of the dicranocoelium type (sensu Näsmark, 1937) in median sagittal section. Oesophagus 0.65-0.72 mm long, musculature of wall developed into a strong muscular bulb in its posterior part; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form dorso-ventral

bends, reach level of acetabulum with the blind ends directed ventrally.

Testes irregular in shape, unlobed or slightly indented, directly or obliquely tandem in posterior half of the body; anterior testis 0.34-0.68 mm long, 0.27-0.45 mm in the dorso-ventral direction; posterior testis 0.29-1.09 mm long, 0.15-0.18 mm in the dorso-ventral direction. Seminal vesicle thin-walled and coiled; pars musculosa relatively well developed, thick-walled and convoluted; pars prostatica 0.15-0.18 mm long and 0.09-0.18 mm wide.

Ovary elongate, 0.15-0.36 by 0.20-0.31 mm, dorsal to posterior testis and anterior to acetabulum; Mehlis' gland close to ovary, 0.11-0.13 by 0.15-0.16 mm; uterus winds forward, dorsal to the testes then ventral to the male ducts; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface about 0.15-0.29 mm anteriorly to the excretory pore; vitellaria in lateral fields, extend from level of pharynx to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 135-141 by 65-72 µm.

Genital pore opens on the ventral surface at level of the oesophagus; terminal genitalium of the parvipapillatum type (new type) characterized by the absence of both genital sphincter and sphincter papilla and the presence of small tegumental papillae on the wall of the genital fold.

Excretory vesicle dorsal or antero-dorsal to acetabulum; excretory pore opens on the dorsal surface posteriorly to the Laurer's canal opening.

FIGURE 147

Orthocoelium parvipapillatum (Stiles and Goldberger, 1910) n. comb.

a - b. Whole worms, sagittal view

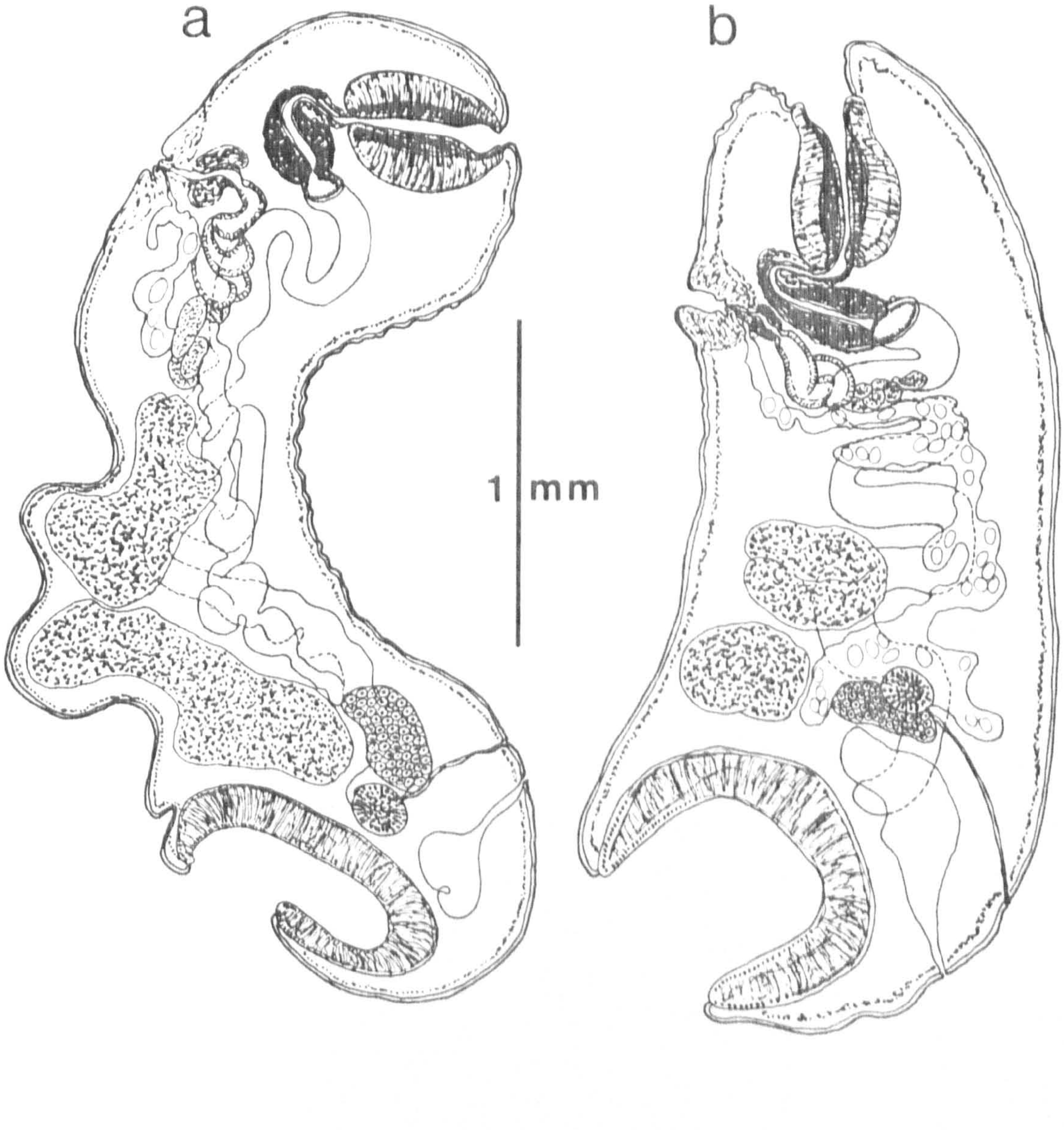

a
b
1 mm

FIGURE 148

Orthocoelium parvipapillatum (Stiles and Goldberger, 1910) n. comb.
(sagittal section)

a. Acetabulum (streptocoelium type), median section.

b. Pharynx (dicranocoelium type) and oesophagus, median section.

c. Pharynx in a more lateral section, note the presence of a lip sphincter in this section.

d. Terminal genitalium (parvipapillatum type), retracted form.

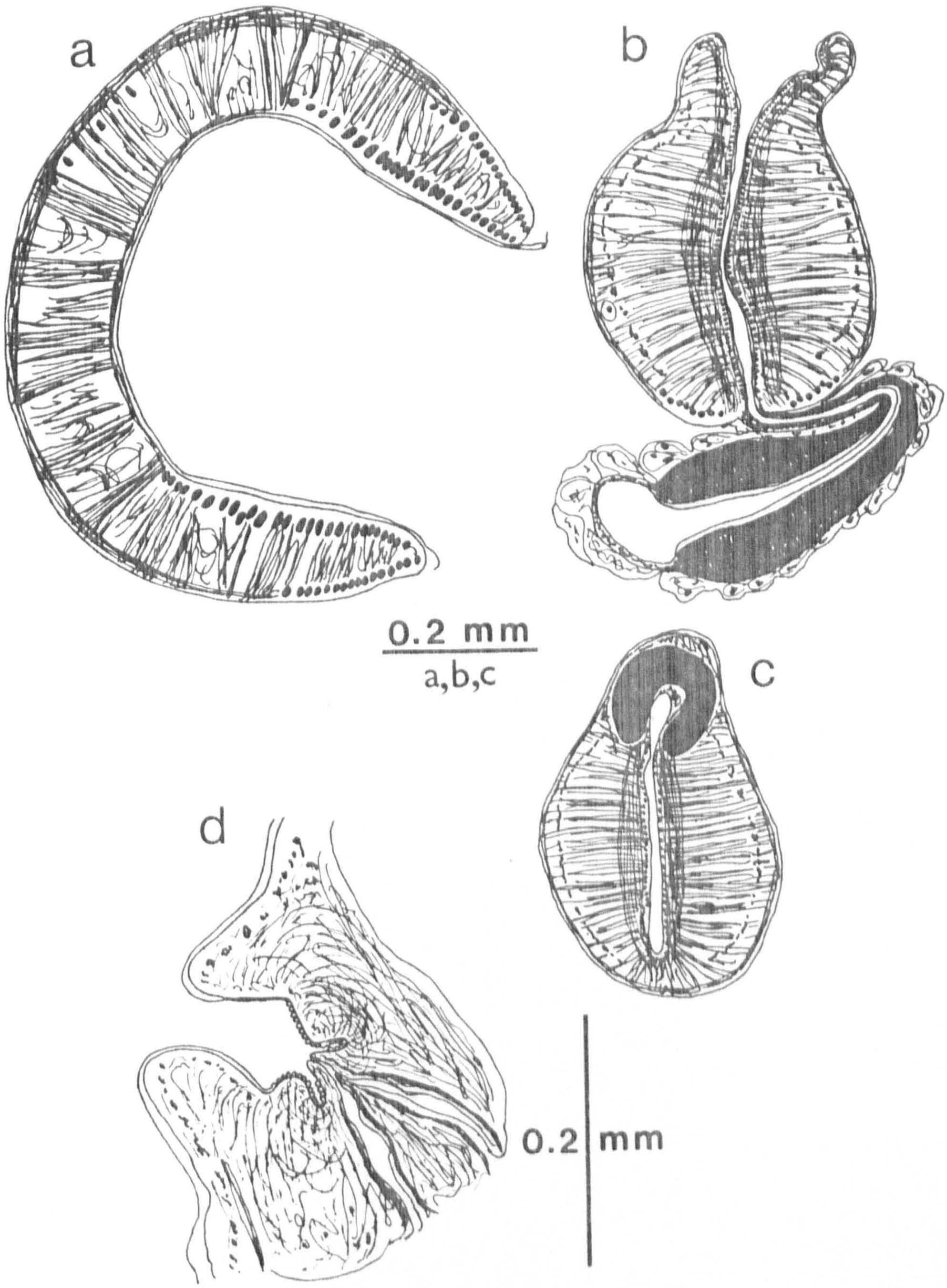

a
b
0.2 mm
a,b,c
c
d
0.2 mm

FIGURE 149

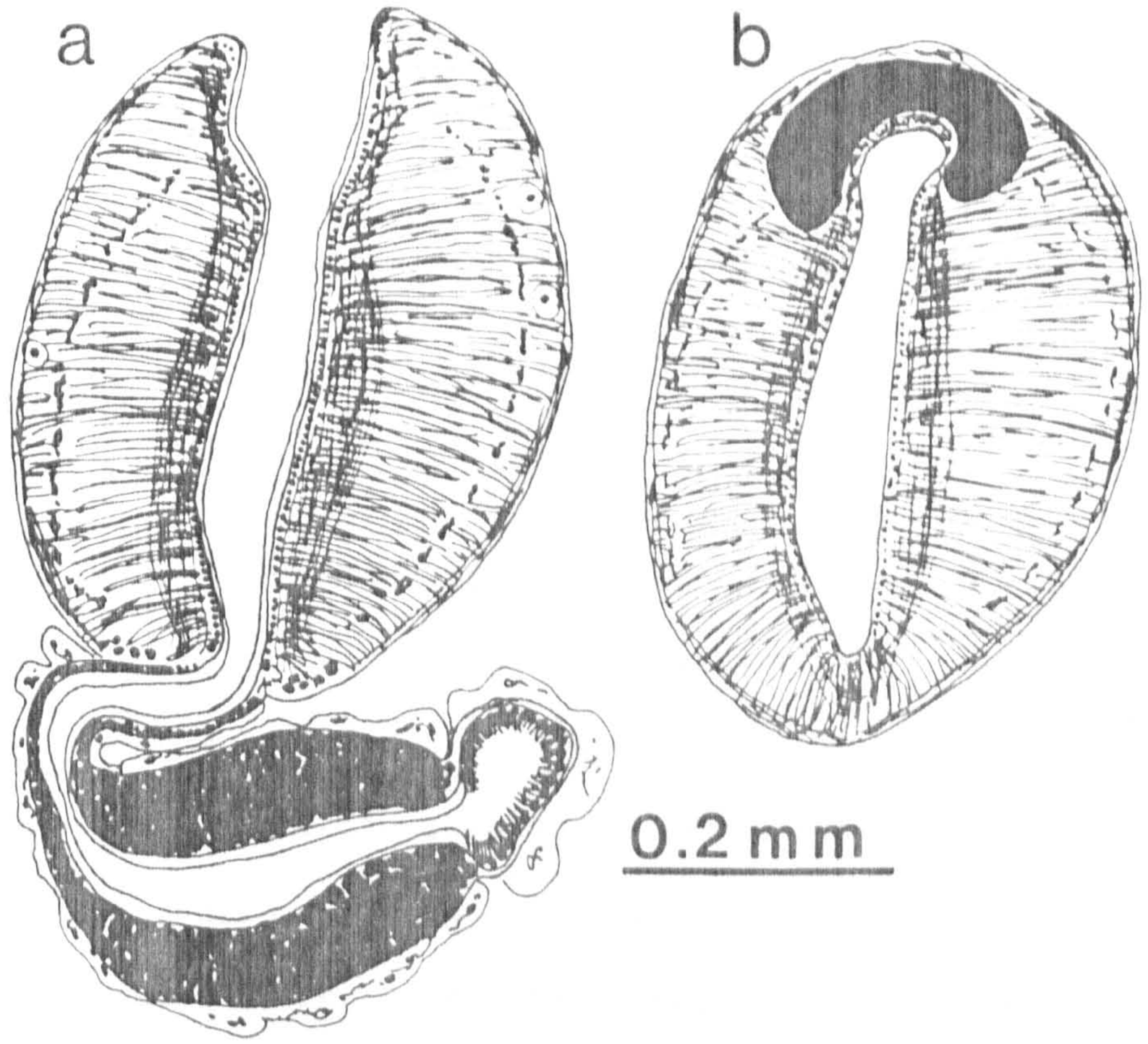
Orthocoelium parvipapillatum (Stiles and Goldberger, 1910) n. comb.
(sagittal section)

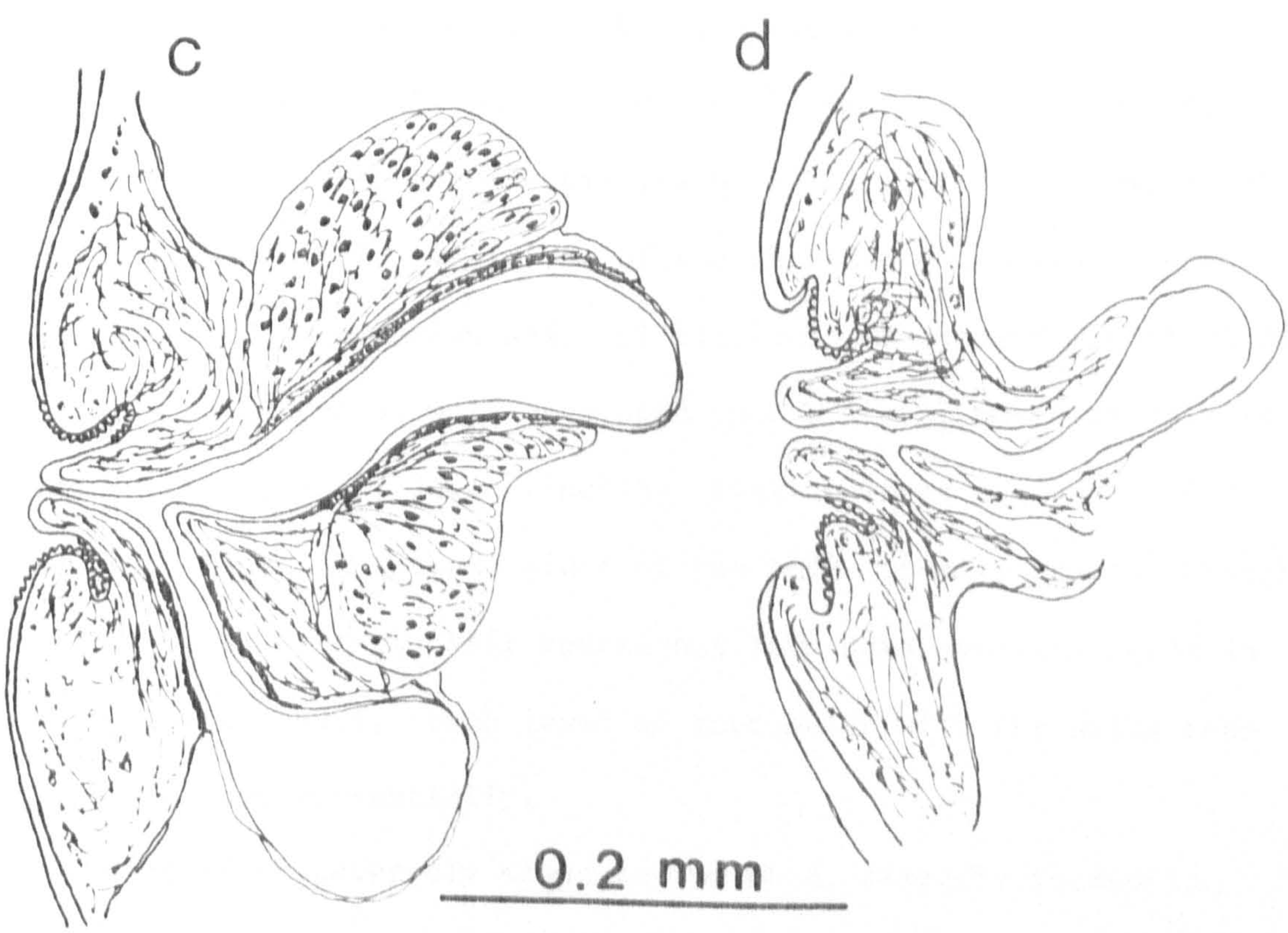
a. Pharynx (dicranocoelium type) and oesophagus, median section. Note that in this section the lip sphincter of the pharynx can not be seen.

b. Pharynx in a more lateral section, note the presence of a lip sphincter.

c. Terminal genitalium (parvipapillatum type), relaxed form and pars prostatica, median section.

d. Terminal genitalium (parvipapillatum type), slightly retracted form, median section.


a
b
0.2 mm


c
d
0.2 mm

Orthocoelium dawesi (Gupta, 1958) Yamaguti, 1971

TYPE SPECIMENS: Not available for examination

MATERIAL EXAMINED: Host, locality and donor/collection

Cattle	India	London School of Hygiene & Tropical Medicine coll. no. 365.

HABITAT: Rumen

DESCRIPTION:

Body small, conical, 2.86-4.51 mm long, 1.81-2.75 mm in greatest width in the dorso-ventral direction.

Acetabulum subterminal, 0.38-0.88 mm in external diameter in the dorso-ventral direction; ratio to body length 1:3.3 to 1:5.6; of the streptocoelium type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 12-17; d.i.c., 20-29; v.e.c., 12-17; v.i.c., 20-26; m.e.c., 7-11.

Pharynx 0.51-0.82 mm long, 0.37-0.54 mm in the dorso-ventral direction; ratio to body length 1:4.6 to 1:7.9, to the diameter of the acetabulum 1:1.2 to 1:1.6; of the dicranocoelium type (sensu Näsmark, 1937) in median sagittal section. Oesophagus 0.40-1.04 mm long, musculature of wall developed into a strong muscular bulb in its posterior part; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, usually nearly straight in the first half of their course but form dorso-ventral bends in the posterior half, reach level of acetabulum with the blind ends directed postero-ventrally.

Testes transversely elongate, unlobed, directly tandem in posterior half of the body; anterior testis 0.35-0.50 mm long, 1.02-1.65 mm in the dorso-ventral direction; posterior testis

0.45-0.66 mm long, 0.85-1.30 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa strongly developed, thick-walled and convoluted; pars prostatica 0.17-0.32 mm long and 0.17-0.20 mm wide.

Ovary subspherical, 0.20-0.36 by 0.20-0.51 mm, postero-dorsal to testes and antero-dorsal to acetabulum; Mehlis' gland close to ovary, 0.20-0.32 by 0.17-0.40 mm; uterus winds forward, dorsal to testes then ventral to the male ducts; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface about 0.45-0.64 mm anteriorly to the excretory pore; vitellaria in lateral fields, extend from level of pharynx to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 100-147 by 60-76 µm.

Genital pore opens on the ventral surface at level of the oesophagus; terminal genitalium of the dawesi type (new type) in median sagittal section characterized by the presence of a round to oval genital sphincter and absence of a sphincter papilla.

Excretory vesicle dorsal to acetabulum and medial to ovary and Mehlis' gland; excretory pore opens on the dorsal surface posteriorly to the Laurer's canal opening.

FIGURE 150

Orthocoelium dawesi (Gupta, 1958) Yamaguti, 1971

a. Whole worm, ventral view

b. Whole worm, sagittal view

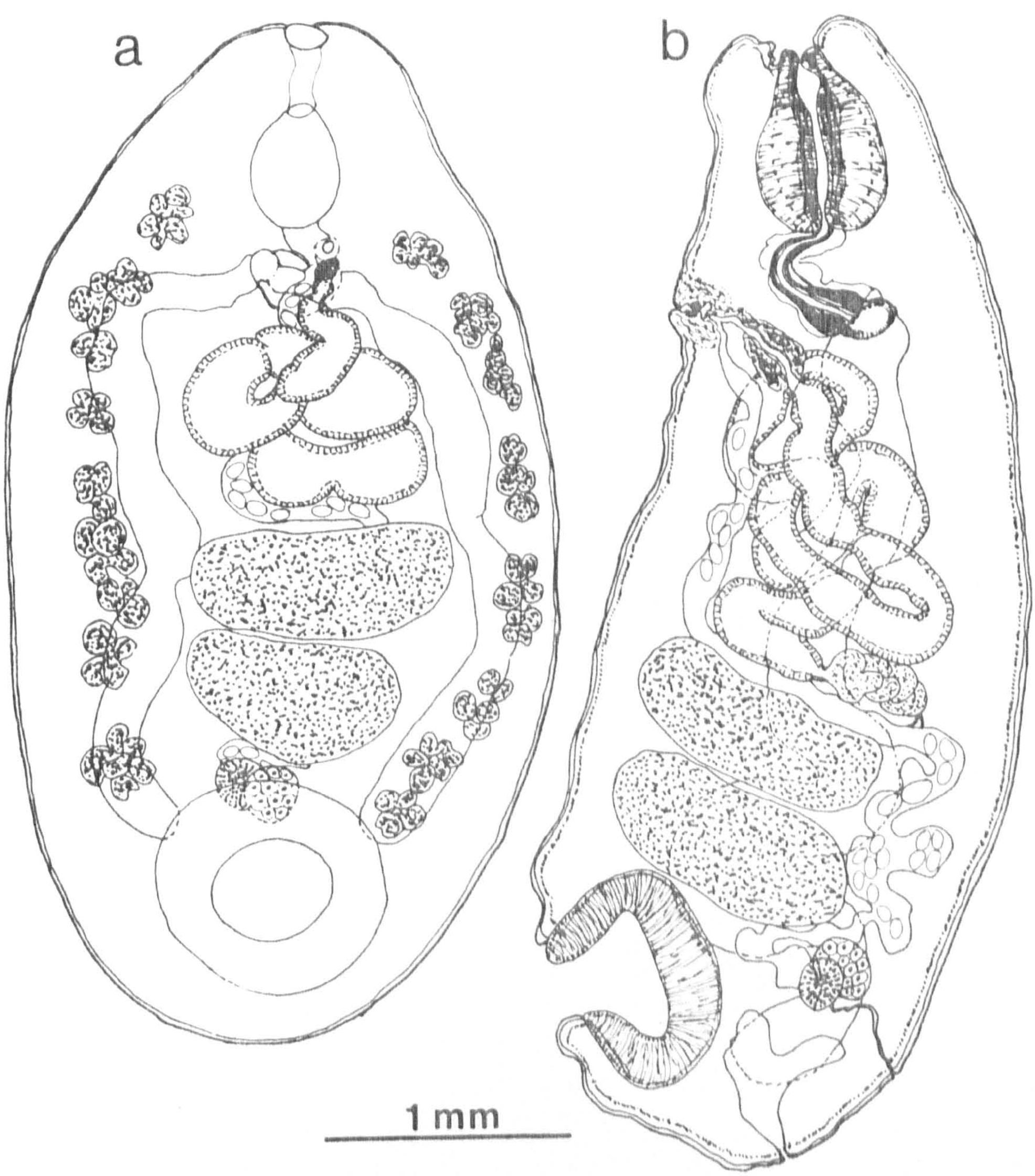

a
b
1 mm

FIGURE 151

Orthocoelium dawesi (Gupta, 1958) Yamaguti, 1971

(sagittal section)

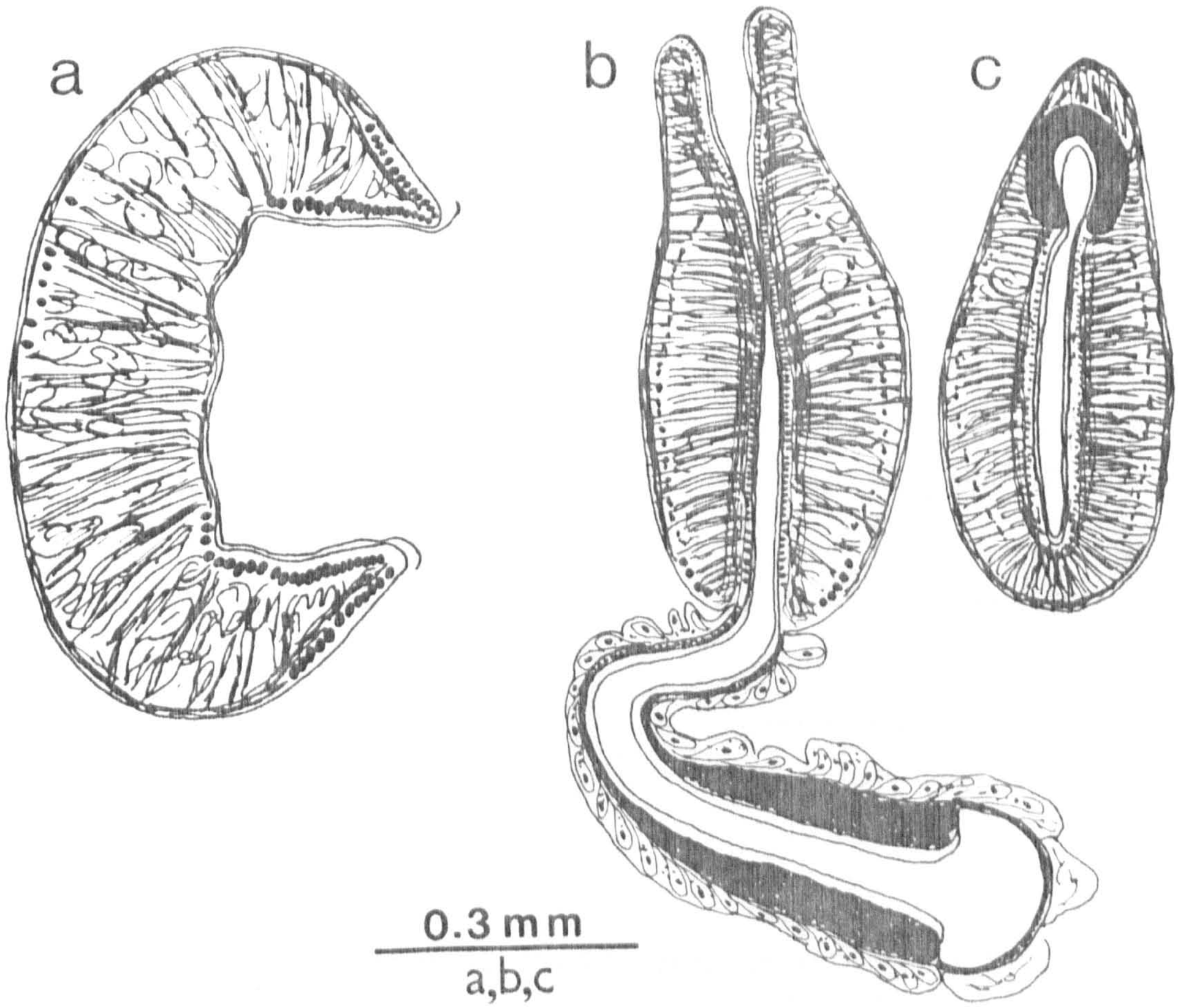
a. Acetabulum (streptocoelium type), median section.

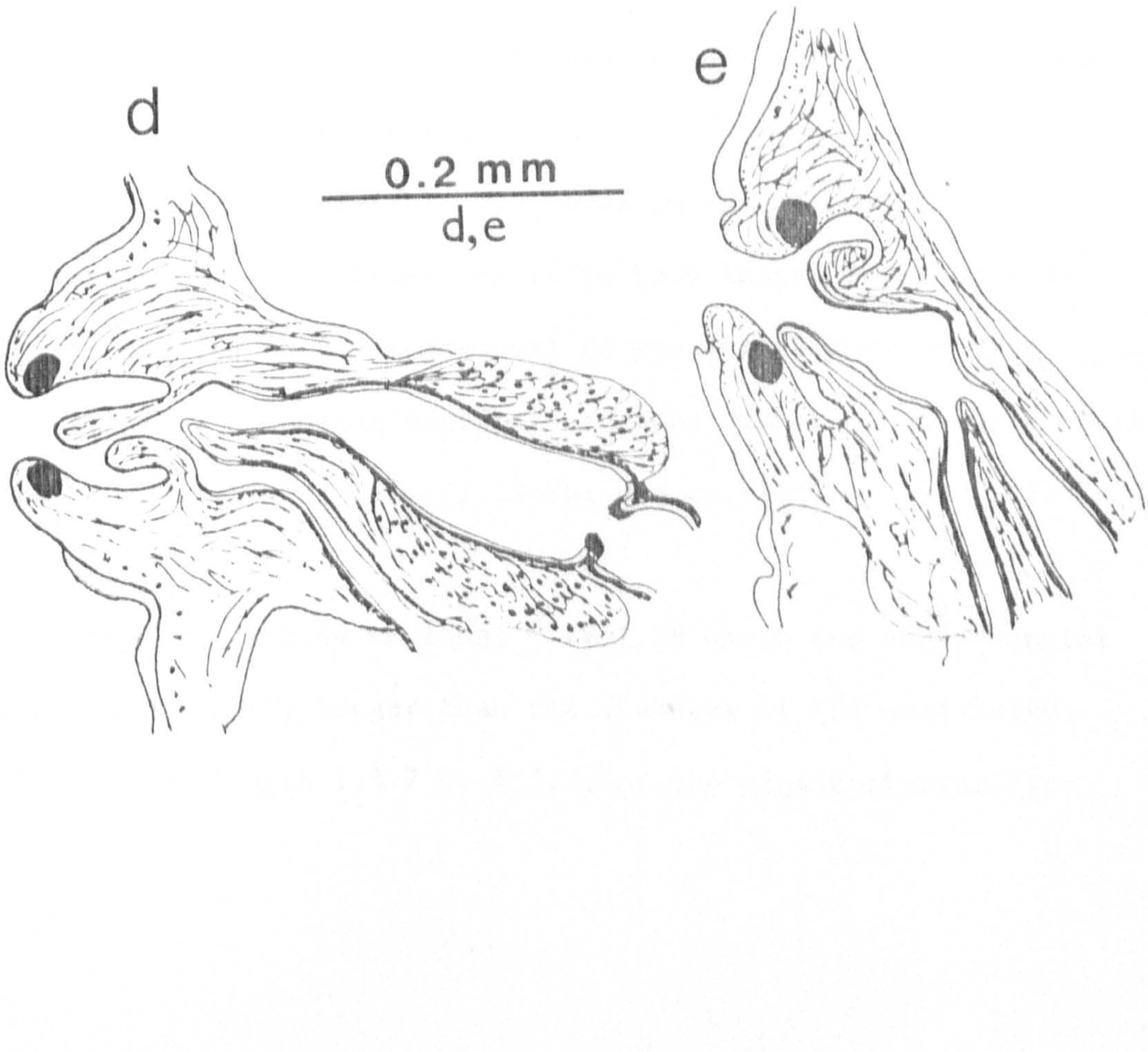
b. Pharynx (dicranocoelium type) and oesophagus, median section.

c. Pharynx in a more lateral section, note the presence of lip sphincter in this section.

d. Terminal genitalium (dawesi type) and pars prostatica.

e. Another terminal genitalium (dawesi type), median section.


a
b
c
0.3 mm
a,b,c


d
0.2 mm
d,e
e

Orthocoelium gigantopharynx (Schad, Kuntz, Anteson and Webster, 1964) n. comb.

Synonym: Paramphistomum gotoi of Dawes, 1936; of Tandon, 1955; and of Lee and Lowe, 1971

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collections

Bubalus bubalis	Jesselton, Sabah Malaysia	British Museum (Natural History) coll. no. 1962. 7.1281-89, labeled "P. gotoi".
	Kuala Lumpur, Malaysia	Dr. Kein Siew Lee
	Philippines	Author's own collection

HABITAT: Rumen

DESCRIPTION:

Body conical, elongate, usually broader anteriorly than posteriorly. Body surface has small papillae randomly arranged on the anterior end around the oral opening and on the posterior end around the acetabular opening.

Acetabulum subterminal, 0.87-1.48 mm in external diameter in the dorso-ventral direction; ratio to body length 1:5.2 to 1:8.1, slightly smaller than the pharynx; of the streptocoelium type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 12-18; d.i.c., 21-28; v.e.c., 11-15; v.i.c., 22-28; m.e.c., 4-9.

Pharynx 1.21-1.64 mm long, 0.78-1.28 mm in the dorso-ventral direction, slightly longer than the diameter of the acetabulum; ratio to body length 1:3.7 to 1:5.7; of the gigantopharynx type

(new type) in median sagittal section characterized by the absence of a middle circular muscle series, absence of interior longitudinal fibres but presence of very fine longitudinal fibres in a small area on its base and presence of long conically pointed and curved papillae lining the anterior half of its internal surface. Oesophagus 0.70-1.19 mm long, musculature of wall moderate in thickness but thickened in its posterior end to form a small sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form deep dorso-ventral bends in their course, each blind end crosses the dorso-median line at the region posterior to the ovary and Mehlis' gland and anterior to the acetabulum to end in each opposite lateral side.

Testes lobed, tandem in posterior two third of the body; anterior testis 0.43-1.48 mm long, 0.75-1.43 mm in the dorso-ventral direction; posterior testis 0.43-1.38 mm long, 0.46-1.46 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa thick-walled, relatively well developed and convoluted; pars prostatica 0.26-0.35 mm long and 0.20-0.22 mm wide.

Ovary subspherical, 0.17-0.56 by 0.29-0.34 mm, posterior to testes; Mehlis' gland close to ovary, 0.25-0.35 by 0.20-0.34 mm; uterus winds forward, dorsal to the testes then ventral to the male ducts; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface about 0.55-0.68 mm anteriorly to the excretory pore; vitellaria in lateral fields, extend from level of the oesophageal bifurcation to anterior border of acetabulum; egg 105-110 by 52-60 µm.

Genital pore opens on the ventral surface at level of the oesophageal bifurcation; terminal genitalium of the microbothrium type (sensu Näsmark, 1937) in median sagittal section but relatively small.

Excretory vesicle narrow and elongate, in the area between acetabulum and ovary; excretory pore opens on the dorsal surface posteriorly to the Laurer's canal opening.

FIGURE 152

Orthocoelium gigantopharynx (Schad, Kuntz, Anteson and Webster, 1964) n. comb.

(SEM)

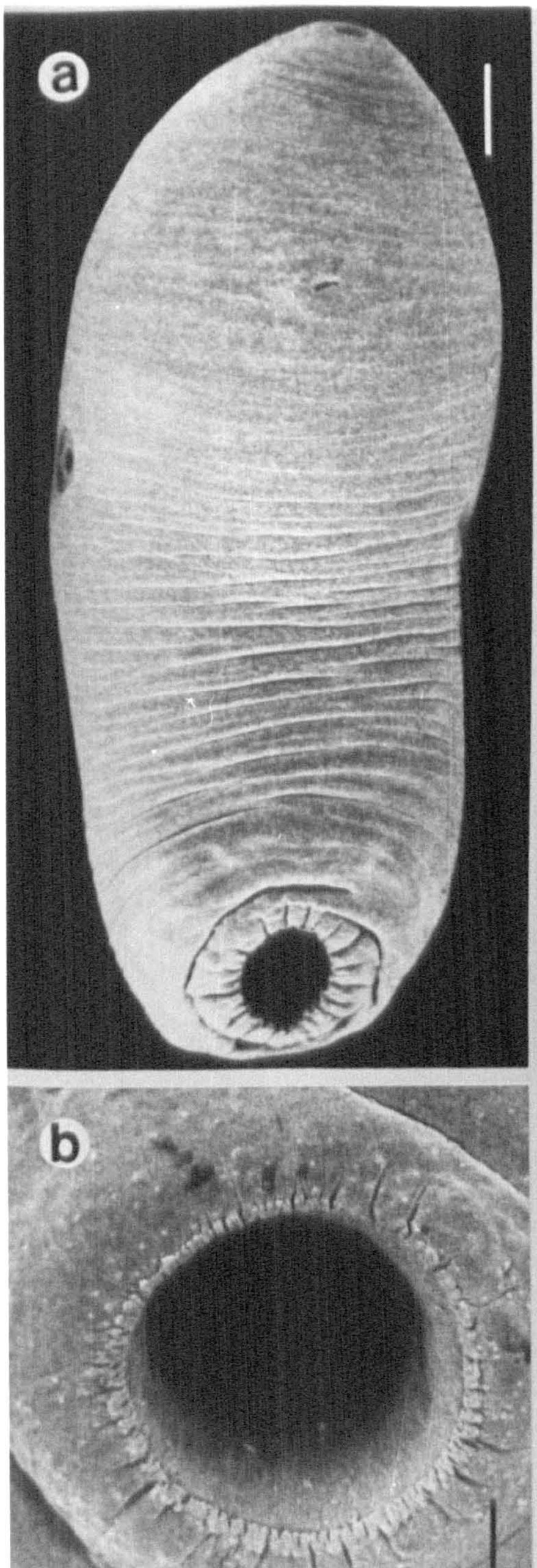
a. Whole worm, ventral view (scale bar = 200 µm)

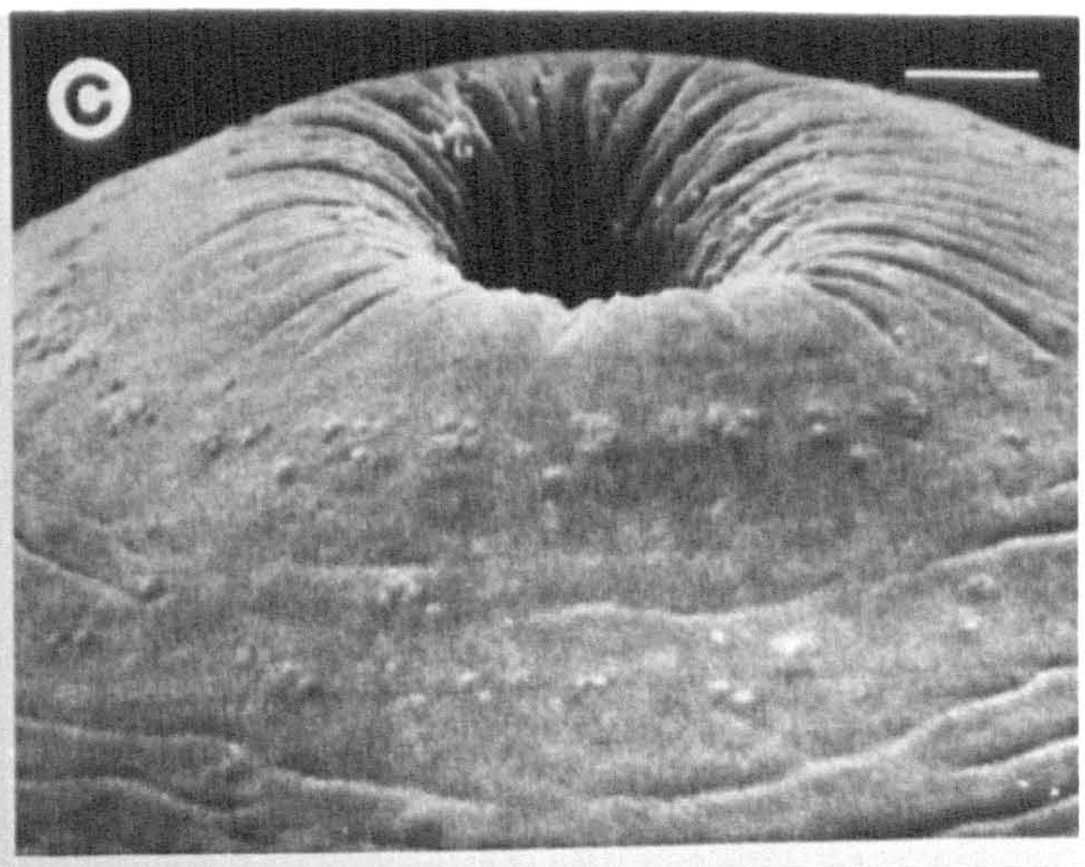
b. Acetabular region, note few papillae (scale bar = 100 µm)

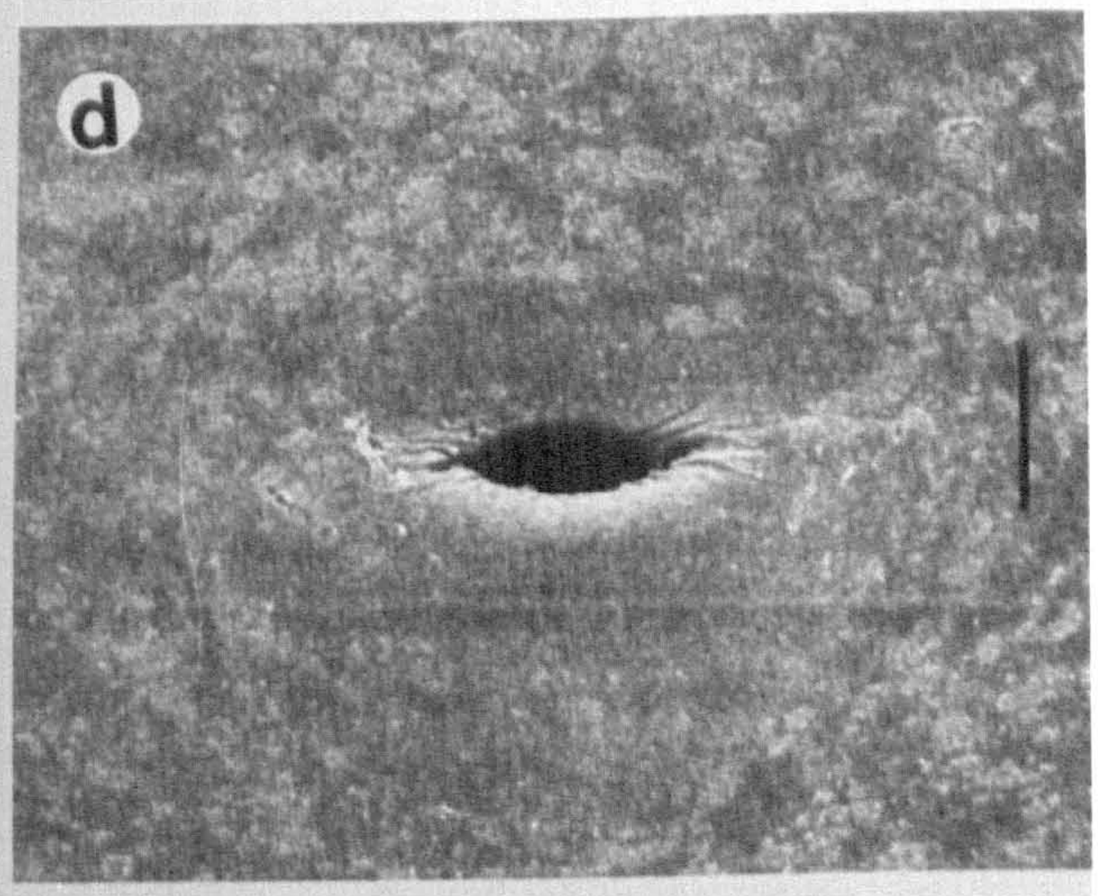
c. Anterior end, note few papillae (scale bar = 30 µm)

d. Genital pore region (scale bar = 50 µm)

e. Another genital pore region with genital papilla partly out (scale bar = 50 µm)


a


c


d

b

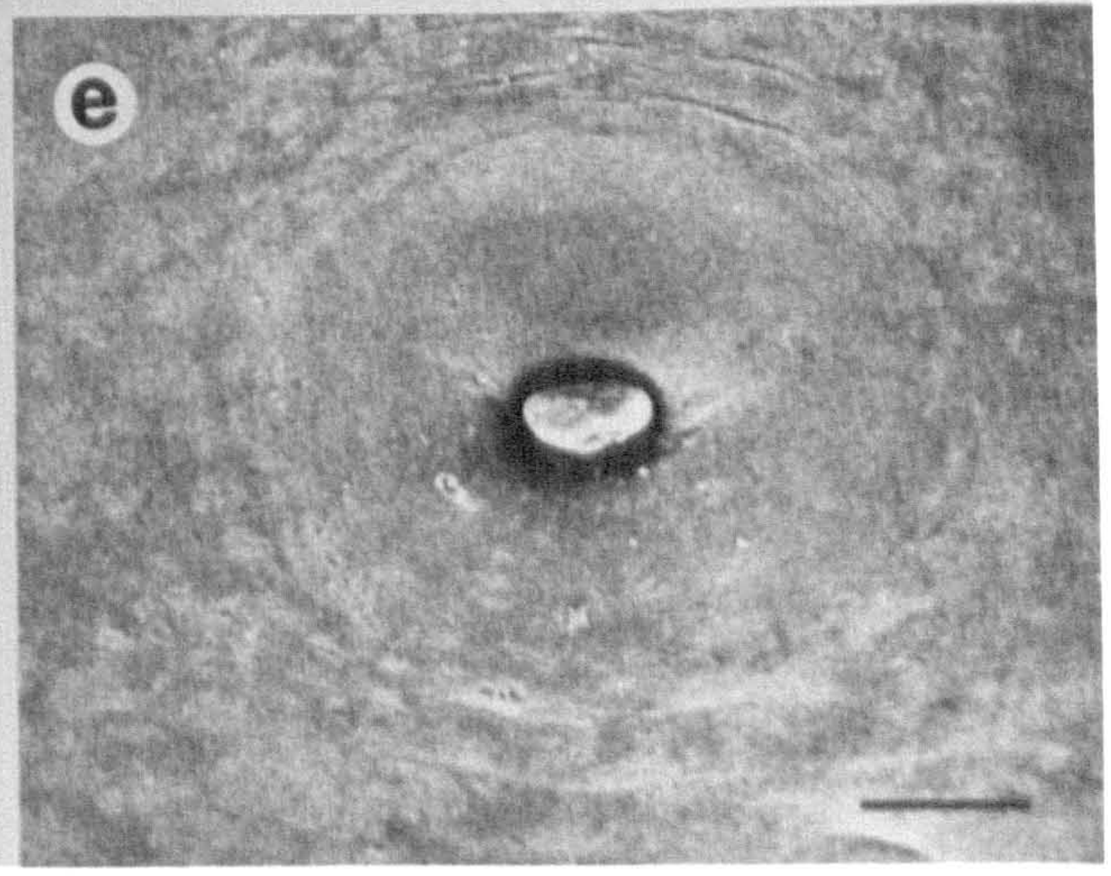

e

FIGURE 153

Orthocoelium gigantopharynx (Schad, Kuntz, Anteson and Webster, 1964) n. comb.

a. Whole worm, ventral view

b. Whole worm, sagittal view

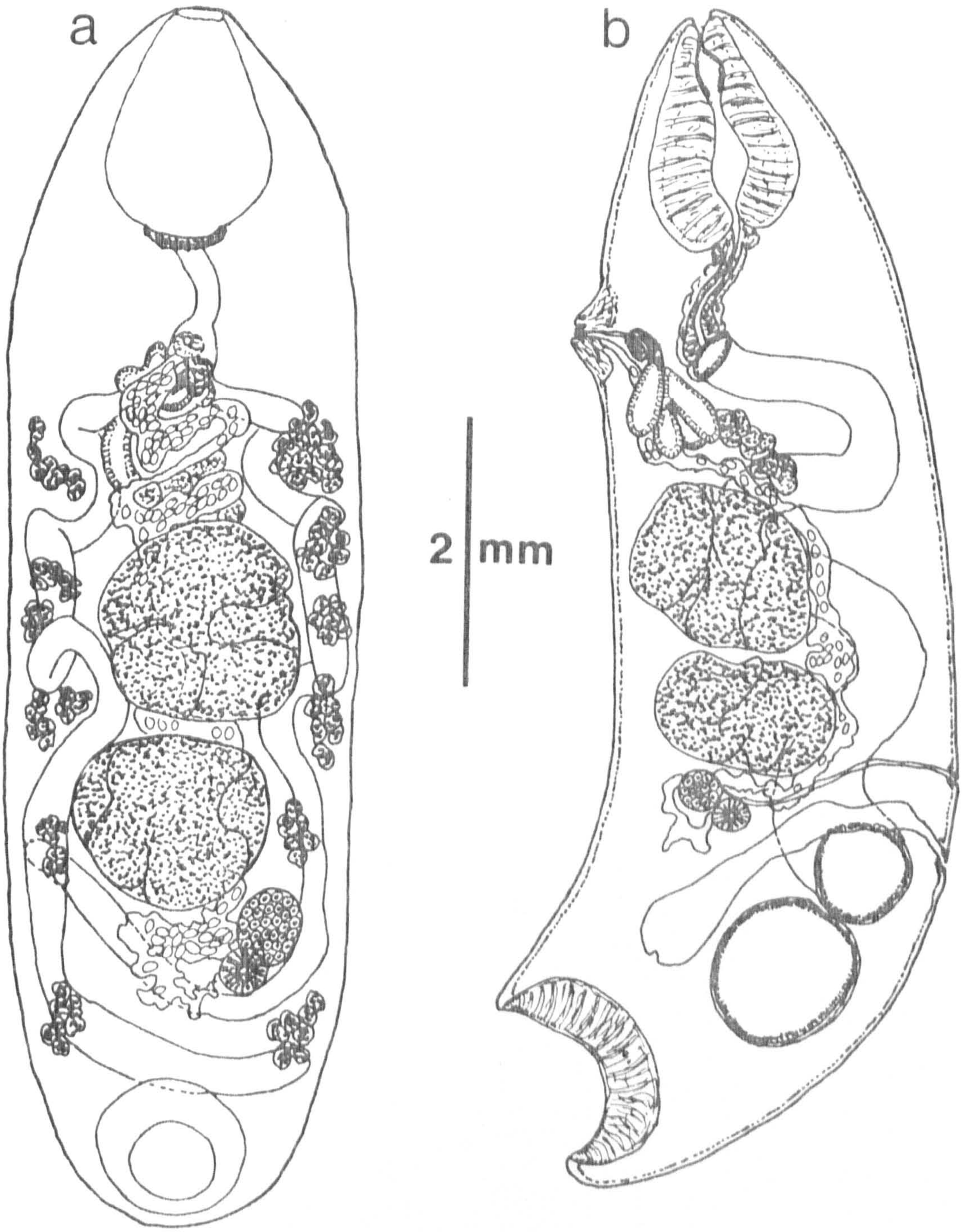

a
b
2 mm

FIGURE 154

Orthocoelium gigantopharynx (Schad, Kuntz, Anteson and Webster, 1964) n. comb.

(median sagittal section)

a. Acetabulum (streptocoelium type)

b. Pharynx (gigantopharynx type) and oesophagus

c - d. Terminal genitalium (microbothrium type) and pars prostatica

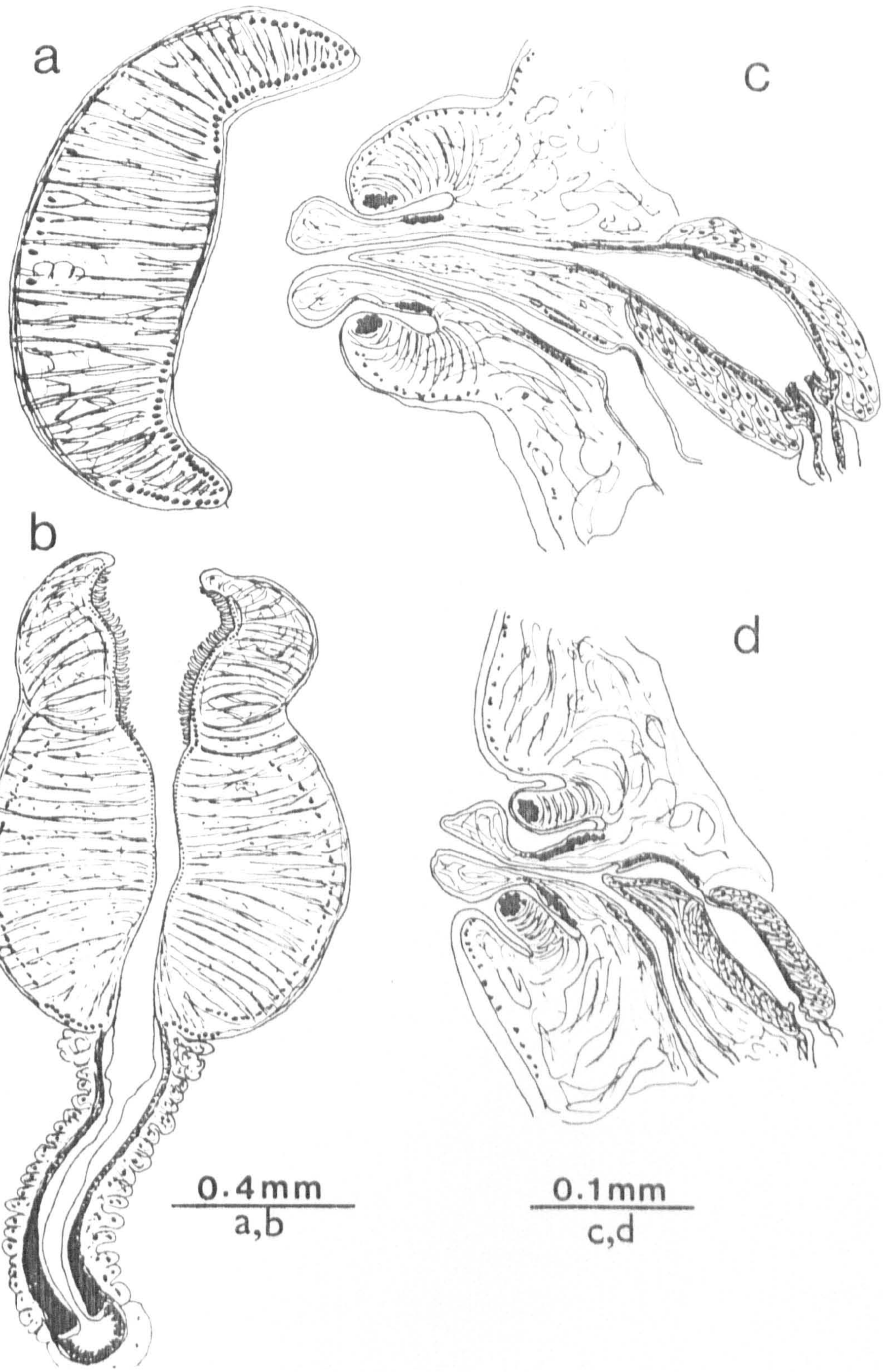

a
b
c
d
0.4mm
a,b
0.1mm
c,d

FIGURE 155

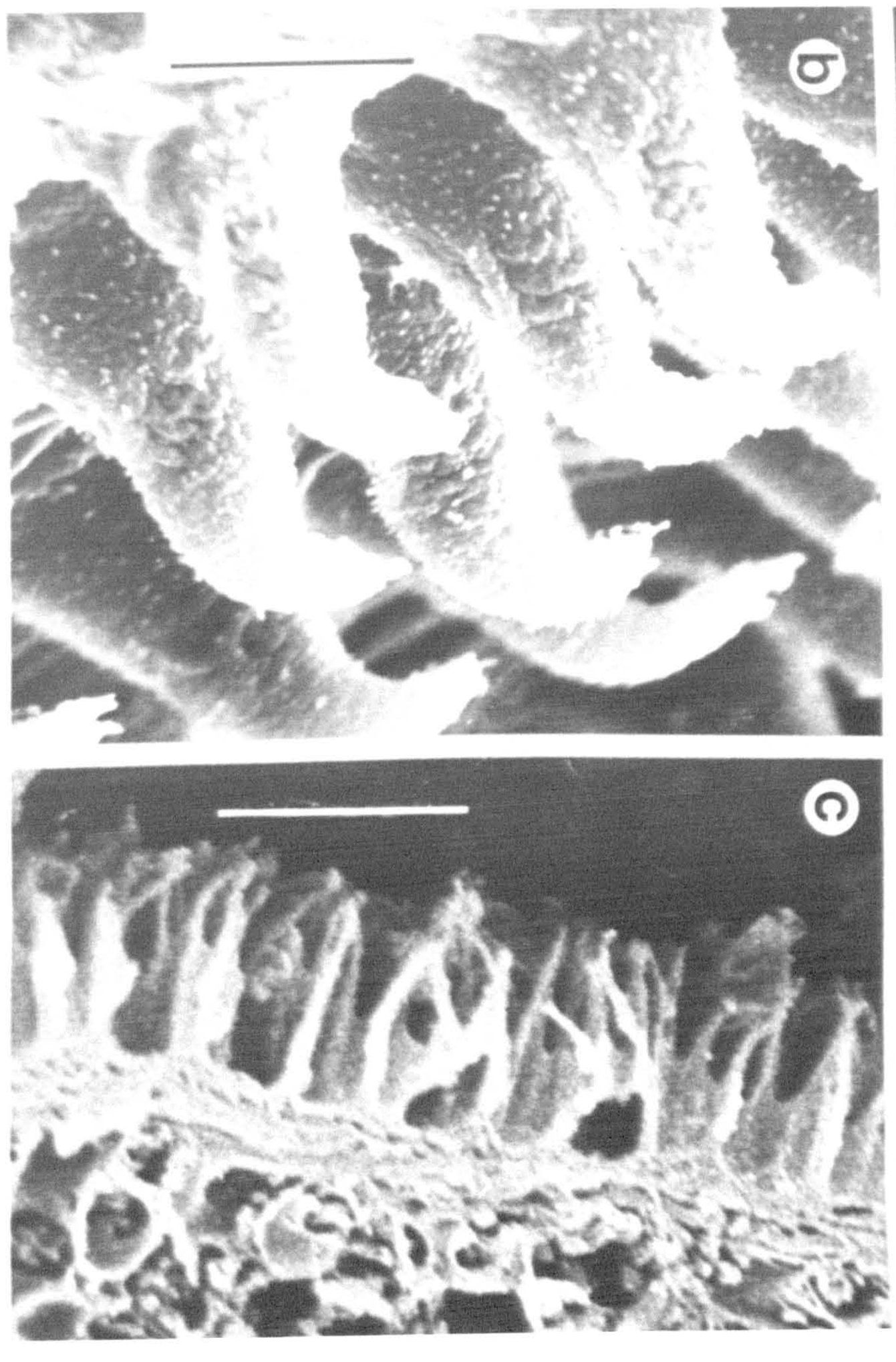
Orthocoelium gigantopharynx (Schad, Kuntz, Anteson and Webster, 1964) n. comb.

Internal surface of pharynx (SEM)

a. General view, note papillae on anterior third of the surface (scale bar = 100 µm)

b. Closer view of papillae on anterior third of the surface (scale bar = 10 µm)

c. Fine hair-like structures lining the surface of the base of the pharynx (scale bar = 10 µm)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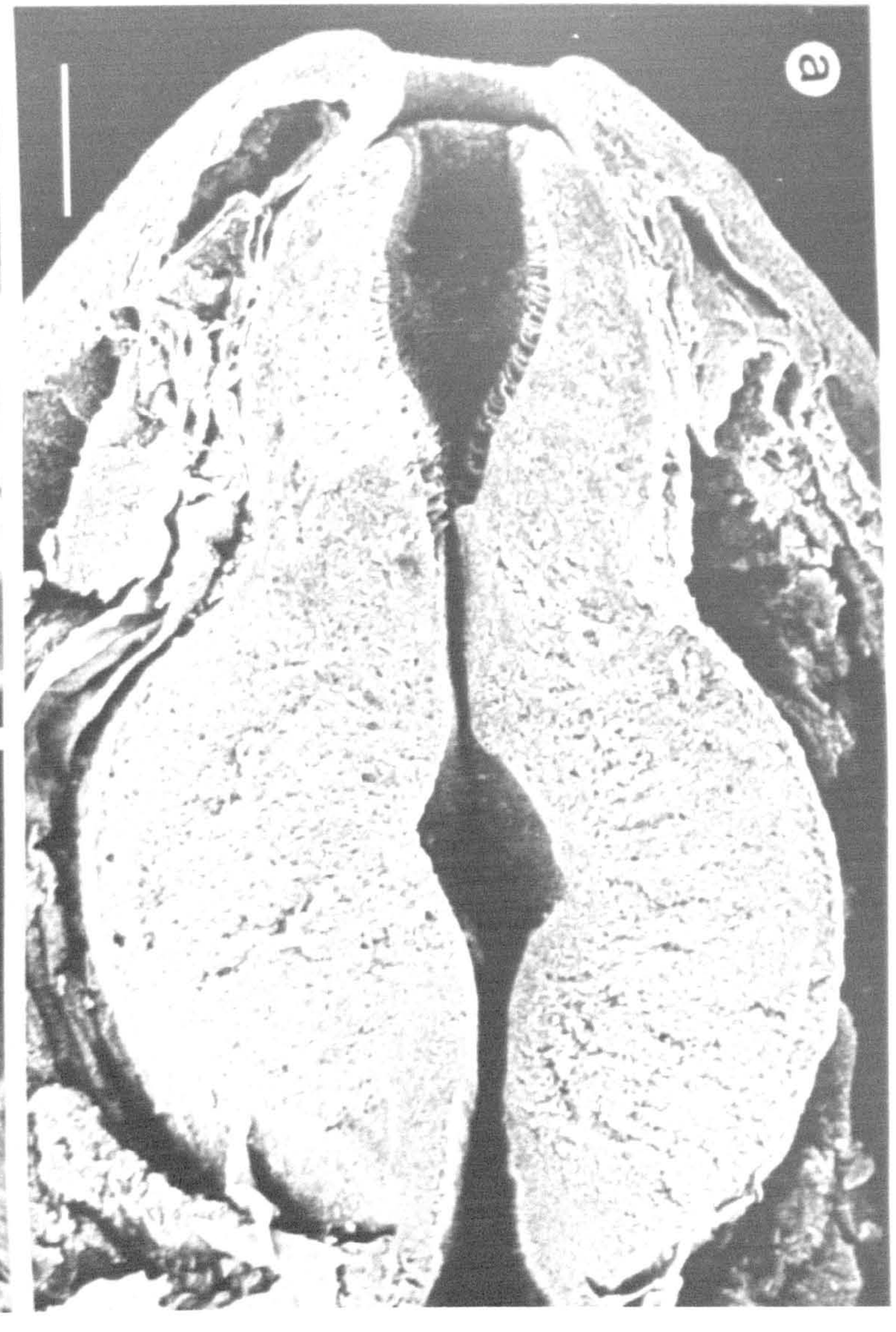
a

Orthocoelium bovini (Gupta and Gupta, 1970) Eduardo, 1980
(= Cochinocotyle bovini Gupta and Gupta, 1970)

TYPE SPECIMENS: Not examined and no other material was available for examination.

HOST: Cattle

LOCALITY: Ernakulam, India

HABITAT: STomach

DESCRIPTION: (Based on Gupta and Gupta, 1970, re-arranged to conform to the format of description given for the rest of the species here.)

Body conical, 5.50-9.54 mm long, 2.30-4.14 mm wide. Body surface smooth.

Acetabulum subterminal, 1.05-2.30 mm in diameter; ratio to body length 1:4.1 to 1:5.2; of the paramphistomum type (sensu Nasmark, 1937) in median sagittal section; number of circular muscle units, d.e.c.1, 14; d.e.c.2, 12; d.i.c., 31-32; v.e.c., 28-29; v.i.c., 21-23; m.e.c. not given.

Pharynx 0.72-0.85 mm long, 0.72-0.74 mm wide; ratio to body length 1:7 to 1:11, to the diameter of the acetabulum, not given; appears to conform with the orthocoelium type in median sagittal section as described earlier in this work; internal surface with papillae. Oesophagus 0.48-0.68 mm long, no bulb or posterior sphincter, lining of internal surface thrown into folds. Caeca in lateral sides of the body, form coils during their course, reach level of acetabulum or short of it.

Testes lobed, tandem in middle third of the body; anterior testis 0.62-0.81 by 0.90 mm; posterior testis 0.33-0.76 by 1.20-1.30 mm. Pars musculosa highly muscular and convoluted.

Ovary triangular in shape, 0.29-0.52 mm in diameter, posterior to the testes and anterior to acetabulum; Mehlis' gland posterior to ovary, 0.34 mm in diameter; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface anteriorly to the excretory pore; vitellaria in lateral fields, extend from level of oesophagus to posterior border of acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg measurement not given.

Genital pore opens on the ventral surface at a level posterior to the oesophageal bifurcation; terminal genitalium of the microbothrium type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle dorsal to acetabulum; excretory pore opens on the dorsal surface posteriorly to the Laurer's canal opening.

Orthocoelium narayanai (Gupta and Gupta, 1972) Eduardo, 1980
(= Ceylonocotyle narayanai Gupta and Gupta, 1972)

TYPE SPECIMENS: Not examined and no other material was available for examination.

HOST: Cattle

LOCALITY: Stomach

HABITAT: Ernakulam, India

DESCRIPTION: (Based on Gupta and Gupta, 1972, re-arranged to conform to the format of description given for the rest of the species here.)

Body conical, 4.95-6.90 mm long, 2.20 mm wide in the dorso-ventral direction.

Acetabulum subterminal, 0.72-0.90 mm in external diameter; ratio to body length 1:5.8 to 1:7; of the calicophoron type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 14-16; d.i.c., 32-34; v.e.c., 12-14; v.i.c., 32-34; m.e.c., not given.

Pharynx 0.54-0.75 mm long, 0.45-0.56 mm wide; ratio to body length 1:7.8 to 1:10, to the diameter of the acetabulum not given; type in median sagittal section not given but illustration and description indicate that it is of the calicophoron type (sensu Dinnik, 1964). Oesophagus 0.27-0.70 mm long, no bulb or posterior sphincter. Caeca in lateral sides of the body, wavy in their course, reach level of acetabulum.

Testes lobed, slightly oblique or almost tandem in posterior half of the body; anterior testis 0.60-0.63 by 0.70-0.72 mm; posterior testis 0.56-0.72 by 0.63-0.72 mm; pars musculosa well developed and convoluted.

Ovary oval, 0.18 by 0.09 mm, posterior to the testes; Mehlis' gland 0.09 by 0.09 mm; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface anteriorly to the excretory pore; vitellaria in lateral fields, not confluent dorso-medially in their anterior or posterior limits; egg 110-130 by 56-60 µm).

Genital pore opens on the ventral surface at a level posterior to the oesophageal bifurcation; terminal genitalium type not given but illustration and description indicate close similarity to the liorchis type (sensu Näsmark, 1937)

Excretory vesicle antero-dorsal to acetabulum; excretory pore opens on the dorsal surface posteriorly to the Laurer's canal opening.

SYSTEMATIC PARASITOLOGY, 1 (3/4), 203–210 (1980).

ORTHOCOELIUM INDONESIENSE, A NEW SPECIES OF AMPHISTOME FROM RUMINANTS IN INDONESIA

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Summary

Orthocoelium indonesiense n. sp. is described from specimens collected from the rumina of *Bos indicus* and *Ovis* sp. in Yogyakarta Special Territory, Indonesia. It is closely related to *Orthocoelium streptocoelium* (Fischoeder, 1901), *O. scoliocoelium* var. *benoiti* (Grétillat, 1966) and *O. narayanai* (Gupta & Gupta, 1972) but can be distinguished from all three by the structure of the acetabulum, genital atrium and oesophagus, the length of the pars prostatica and the extent of the excretory vesicle. *Gastrothylax glandiformis* Yamaguti, 1939 is reported for the first time from Indonesia.

Introduction

A collection of amphistomes from Indonesia was sent to the author for identification by Dr. Wardiarto of the Faculty of Veterinary Medicine, Gadjah Mada University, Indonesia. The specimens were collected from the rumina of *Bos indicus* (zebu) and *Ovis* sp. Two species of pouched amphistomes (Gastrothylacidae), *Fischoederius elongatus* (Poirier, 1883) Stiles & Goldberger, 1910 and *Gastrothylax glandiformis* Yamaguti, 1939 were identified in the collection. As far as the writer is aware, *G. glandiformis* has never been reported from Indonesia before. Careful examination also revealed the presence of specimens of a third, undescribed species in the collection. These specimens were studied as stained whole mounts, thick hand sections and microscopic paraffin sections. Representative specimens were also studied under the scanning electron microscope for surface topography.

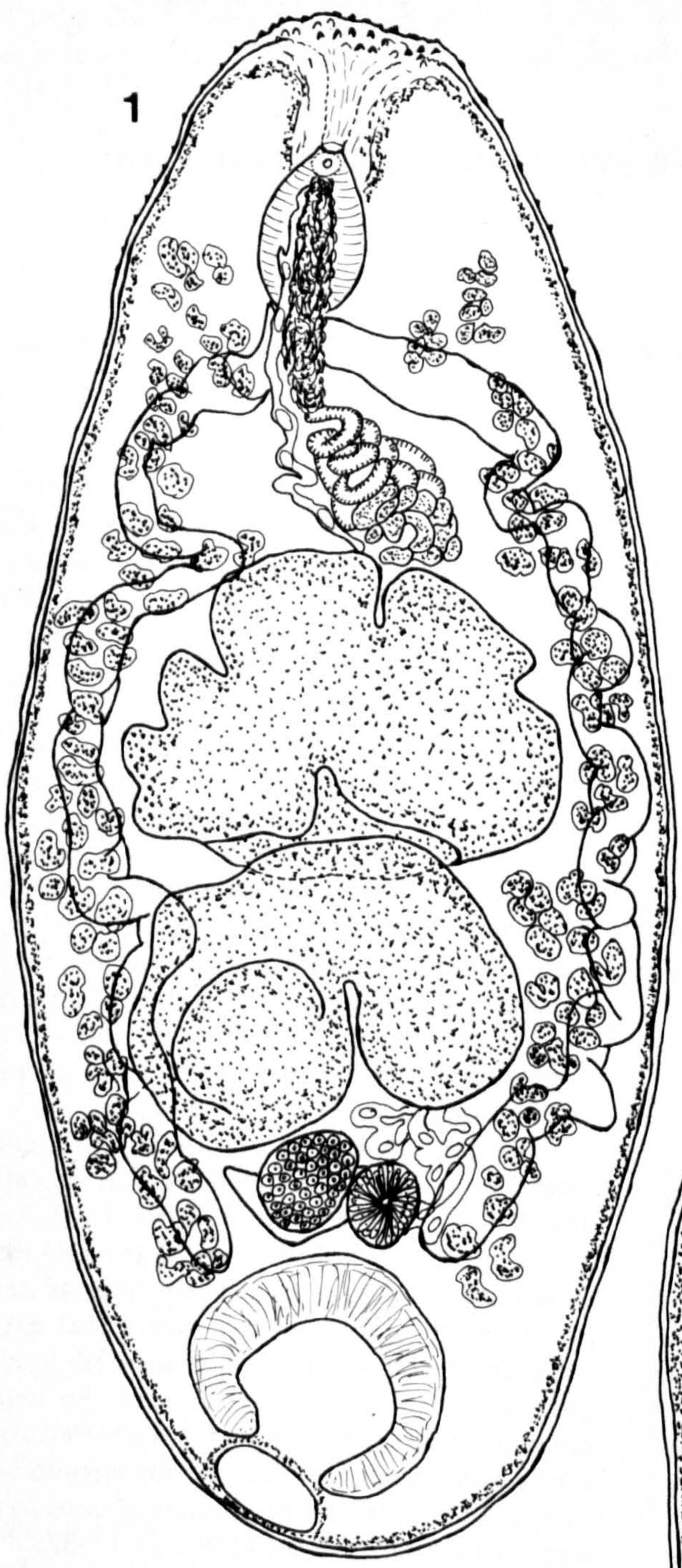
* Supported by a scholarship under the 4th Education Project of the Philippines with the World Bank.

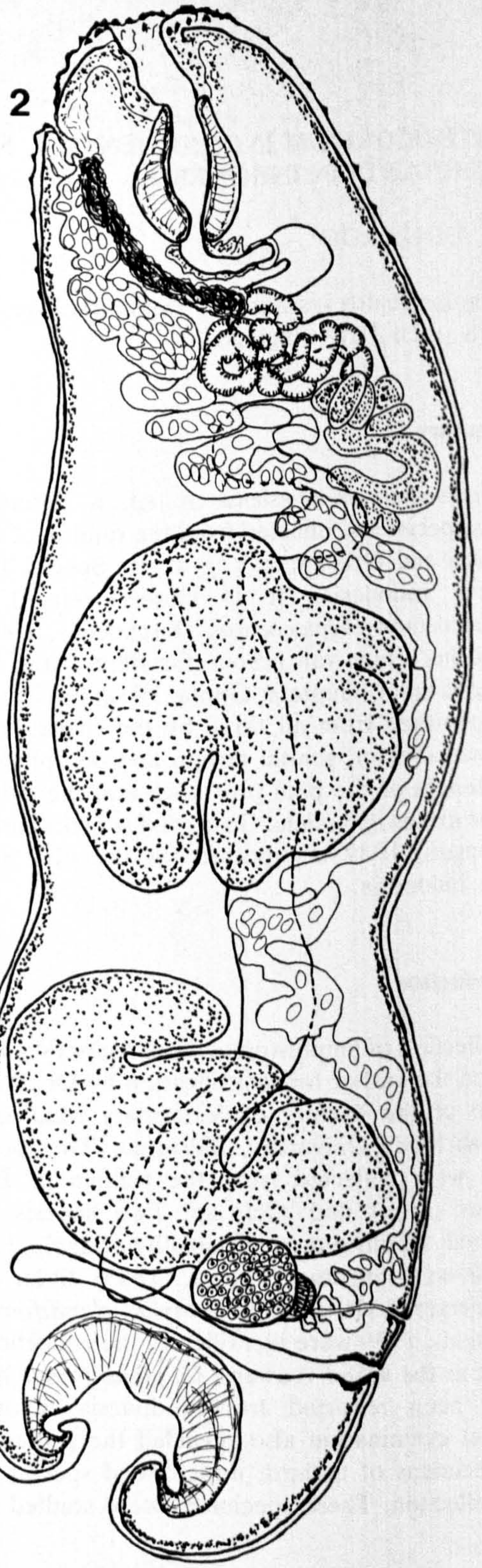
Orthocoelium indonesiense n. sp.

The specimens are subcylindrical in shape (Figs. 1 and 2) and are 4.95 to 7.01 mm long. The greatest diameter attained at the level of the testes is 1.03 to 2.01 mm in dorso-ventral direction. Depending on the state of the worm during fixation, the body appears straight or slightly bent dorsally or ventrally. Scanning electron microscope examination of the body surface revealed the presence of smooth, dome-shaped, tegumental papillae only on the anterior quarter of the body (Plate I).

The acetabulum is terminal, its external diameter is 0.642 to 0.890 mm and its ratio to the length of the body is 1:5.5 to 1:9.4. In median sagittal sections (Fig. 4) the acetabulum is seen to be of the gastrothylax type, as defined by Näsmark (1937), in that the dorsal exterior circular muscle series is not divided into two parts and the number of units in the exterior circular muscle series (dorsal and ventral) consistently exceeds that in the interior circular series (dorsal and ventral). The number of units in each series is: dorsal exterior (DE), 33 to 37; dorsal interior (DI), 20 to 30; ventral exterior (VE), 32 to 44; ventral interior (VI) 22 to 28; dome six to 10.

The pharynx is 0.501 to 0.682 mm long, 0.313 to 0.513 mm in the dorso-ventral direction and its ratio to the length of the body is 1:8 to 1:12.5 and to the diameter of the acetabulum is





1·0 mm

1,2

Orthocoelium indonesiense n.sp.

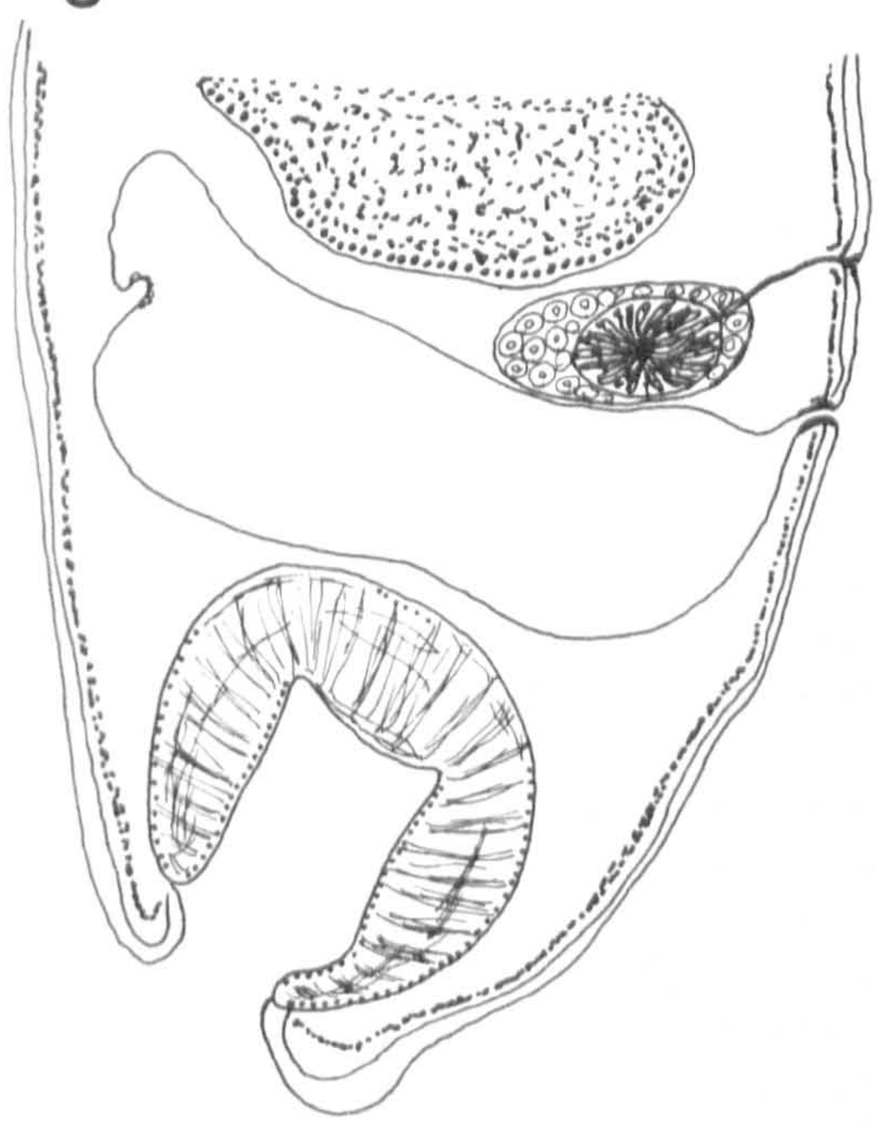
Fig. 1. Whole worm, ventral view

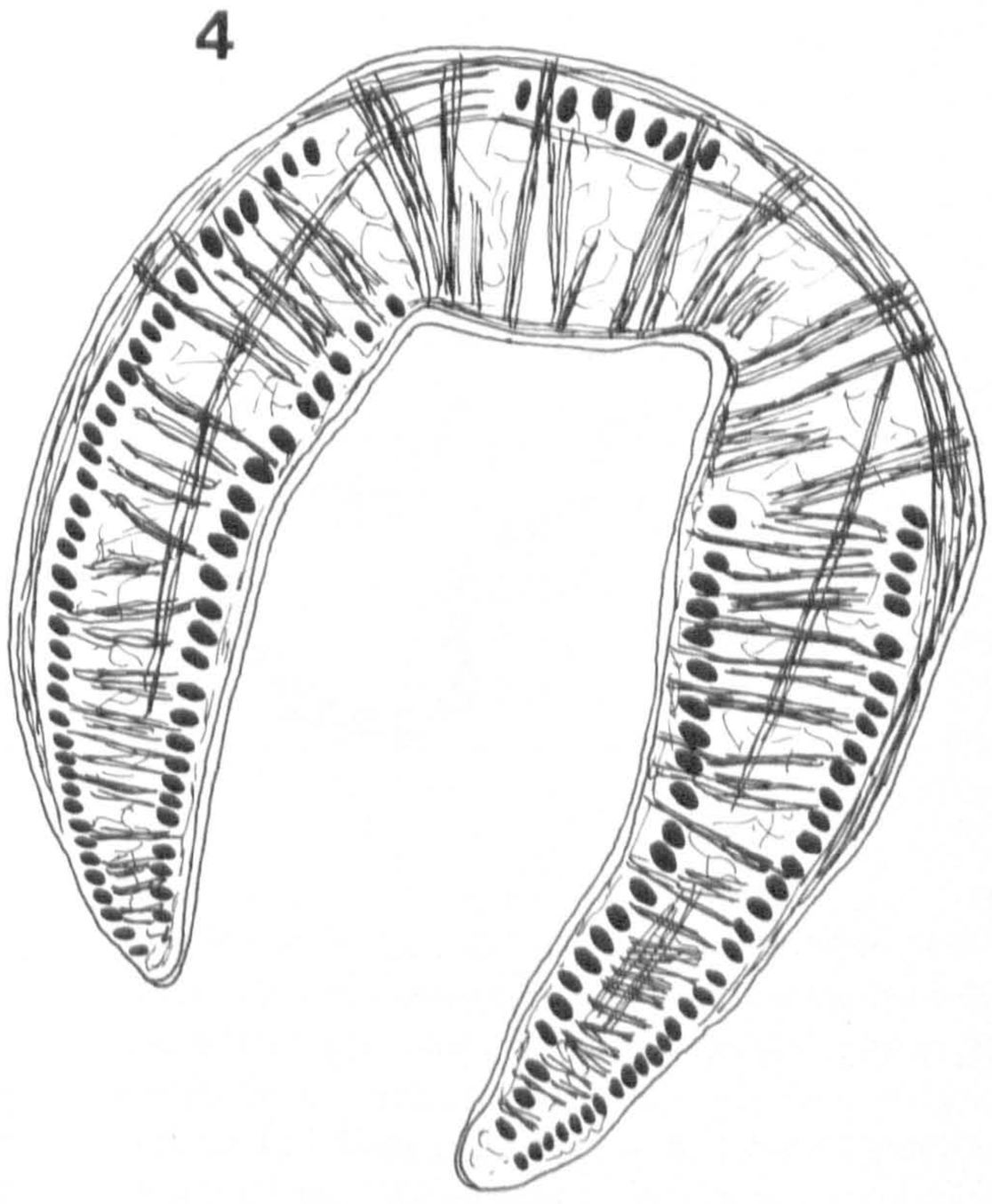
Fig. 2. Whole worm, sagittal view. Note deep excretory vesicle even in collapsed state

1:1.3 to 1:1.6. In median sagittal section (Fig. 5), the pharynx conforms to the paramphistomum type, as described by Näsmark (1937), in that there is no lip, no anterior or posterior sphincters and no middle circular muscle units. The oesophagus is 0.206 to 0.413 mm long; the musculature of its wall is relatively thick and there is no bulbous expansion or posterior sphincter (Fig. 5). The caeca, during their course posteriorly along the lateral sides of the body, form irregular dorso-ventral bends which appear to be more pronounced anteriorly. The blind ends of the caeca terminate just anterior to the acetabulum and are directed posteriorly.

The intercaecal lobed testes (Figs. 1 and 2) lie tandem in position in the posterior two thirds of the body anterior to the ovary and Mehlis' gland. The anterior testis measures 0.702 to 1.534 mm in length, 0.737 to 1.43 mm in width and 0.855 to 1.416 mm in the dorso-ventral direction. The posterior testis measures 0.767 to 1.091 mm in length, 1.003 to 1.180 mm in width and 0.590 to 1.416 mm in the dorso-ventral direction. The pars prostatica is long (0.590 to 0.86 mm) about five to six times as long as it is wide and almost straight (Figs. 1 and 2). The well-developed pars musculosa and the thin walled vesicula seminalis are coiled and lie dorsal to the distal part of the uterus.

The spherical ovary lies in the posterior third of the body, to the left or right of the median line in between the posterior testis and excretory vesicle. It measures 0.206 to 0.354 mm by 0.454 to 0.495 mm. Mehlis' gland is round to oval in outline, lies close to the ovary and measures 0.130 to 0.236 by 0.217 to 0.442 mm. Laurer's

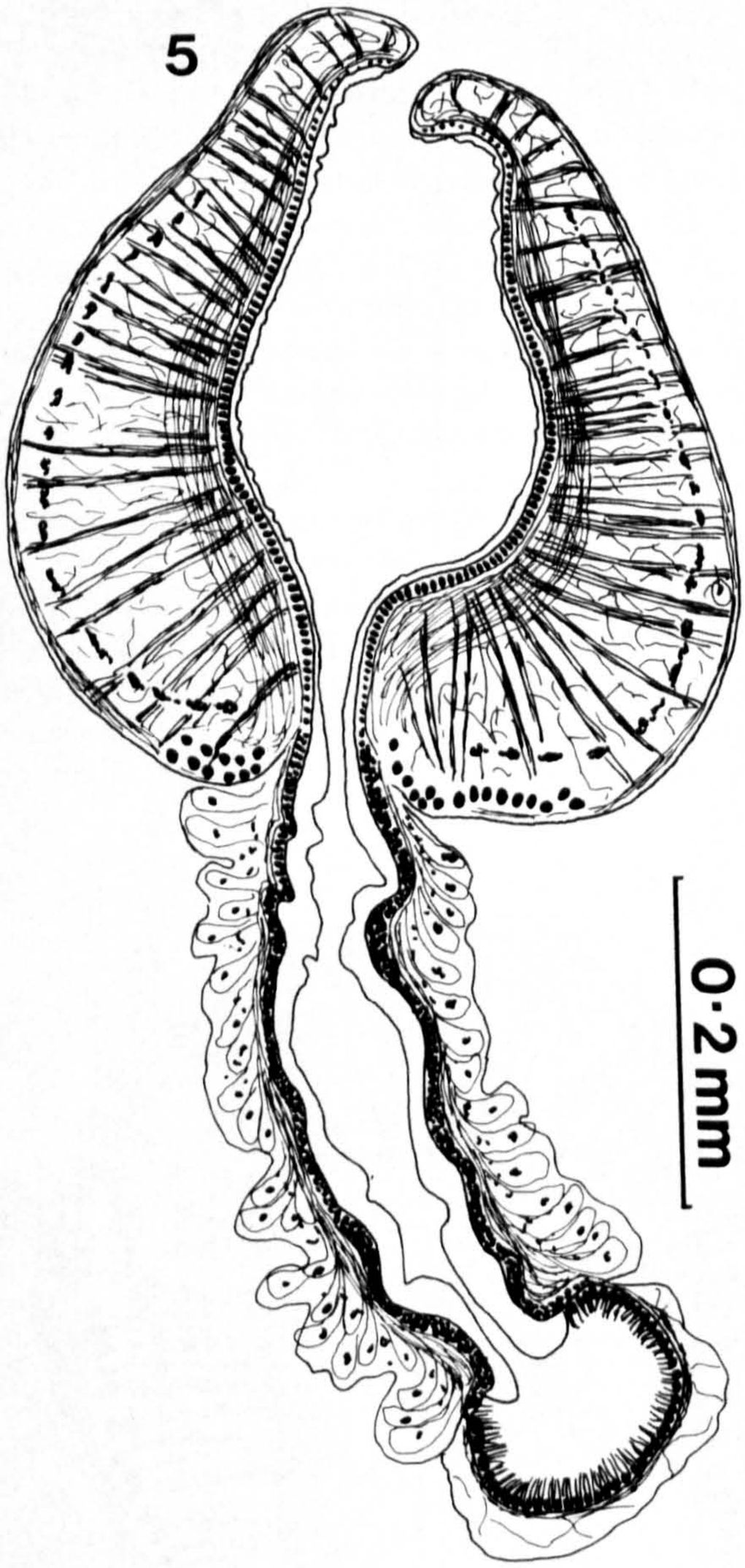


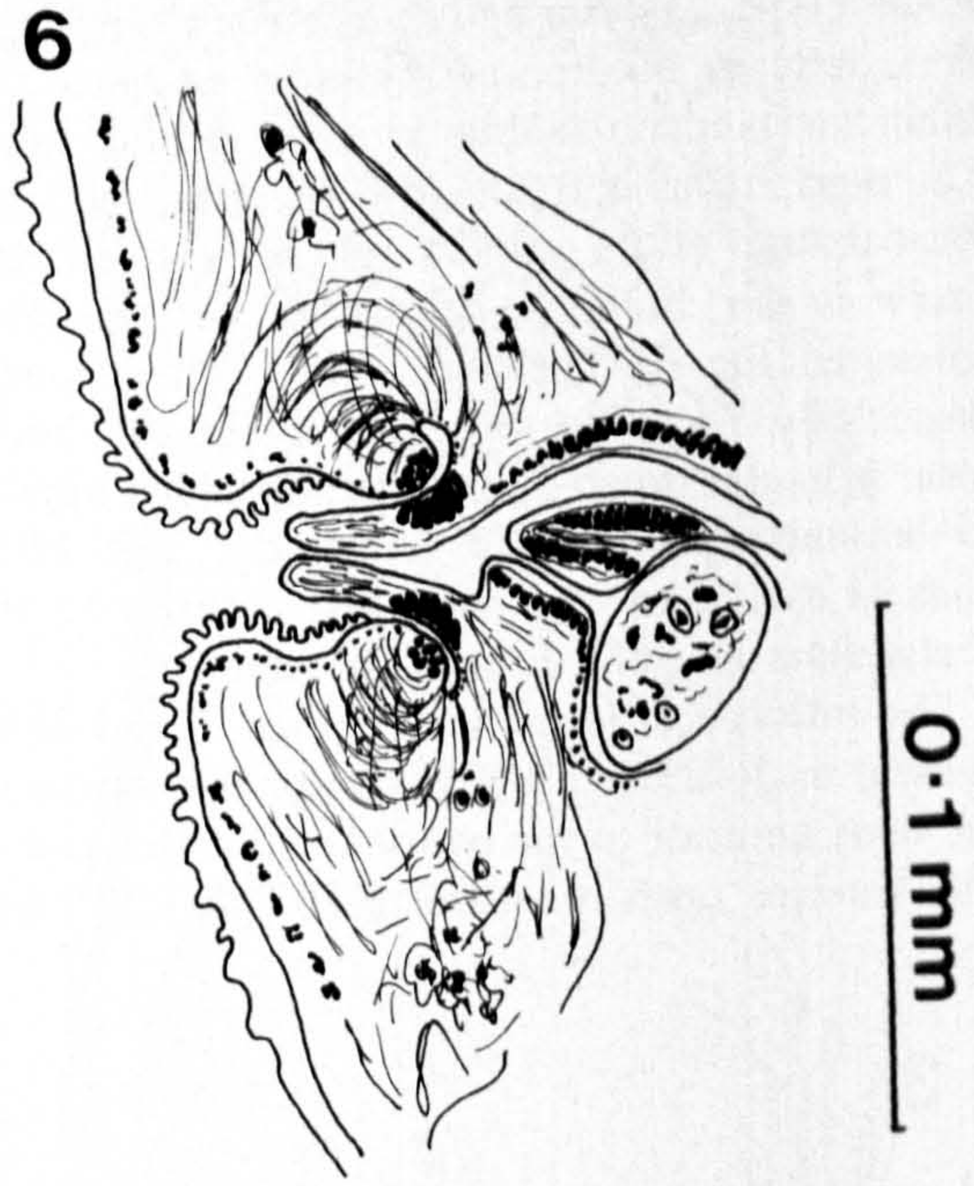


Orthocoelium indonesiense n.sp.

Fig. 3. Posterior part, median sagittal view showing deep excretory vesicle in full state

Fig. 4. Acetabulum, median sagittal section





Orthocoelium indonesiense n.sp.
Fig. 5. Pharynx, median sagittal section
Fig. 6 Genital atrium, median sagittal section

canal emerges from the lateral side of the Mehlis' gland, runs anterior and parallel to the excretory vesicle and opens anterior to the excretory pore on the dorsal surface. The uterus extends forward dorsal to the testes but ventral to the male ducts. The operculate eggs are oval and measure 120 to 137 by 60 to 67 μm. Clusters of vitelline glands extend along the lateral sides from the level of the pharynx to the level of the anterior border of the acetabulum.

The deep excretory vesicle lies anterior to the acetabulum extending near the dorsal wall to near the ventral wall, either in collapse or when full (Figs. 2 and 3). Its duct is very short and the excretory pore opens posterior to the opening of Laurer's canal.

The genital opening lies ventrally at the level of the pharynx about 0.4 to 0.65 mm from the anterior end. The genital papilla, which is moderate in size, lies at the bottom of a narrow and shallow atrium and is surrounded by a distinct genital fold. The atrium carries on its wall tegumental papillae of the same type as those found on the anterior body surface. In median sagittal section (Fig. 6), the genital fold forms a weakly developed genital sphincter but the genital papilla has a well developed sphincter at its base. These features agree with papillogenitalis type of genital atrium as defined by Eduardo (1980).

Discussion

Stiles & Goldberger (1910) proposed *Orthocoelium* as a subgenus of *Paramphistomum* Fischoeder, 1901 because Laurer's canal does not cross the excretory vesicle or duct. For the same reason, Näsmark (1937) erected the genus *Ceylonocotyle*. Price & McIntosh (1953), however, pointed out that *Orthocoelium* has priority over *Ceylonocotyle* since subgenera have the same nomenclatorial status as genera. Yamaguti (1971) emended *Orthocoelium* to full generic status and listed all species previously described as *Ceylonocotyle* under the genus *Orthocoelium*. In his list of nine species he also included *Orthocoelium petrowi* (Davidova, 1959) which was earlier transferred to the genus *Paramphistomum* in a new combination by its original author under her married name (Velichko, 1966) after a careful and more detailed re-examination of the original specimens and study of additional material. Yamaguti apparently was unaware of this paper as it is not included in his bibliography. Two species recently described under *Ceylonocotyle* should also be moved to the genus *Orthocoelium* as new combinations, namely, *Orthocoelium narayanai* (Gupta & Gupta, 1972) and *Orthocoelium tamilensis* (Gupta & Bakhshi *in* Gupta & Nakhasi, 1977).

The present specimens are assigned to the genus *Orthocoelium* (Stiles & Goldberger, 1910) Yamaguti, 1971 on the following grounds: the subcylindrical body shape, Laurer's canal does not cross the excretory vesicle or duct, the pars musculosa is well developed and coiled, the testes are tandem in arrangement and there is no genital sucker. Species of this genus can be differentiated from each other by a combination of characters, including the structure of the pharynx, genital atrium, acetabulum and oesophagus, the length of the pars prostatica and pars musculosa and the character of the caeca. To date, the genus contains 11 species.

The present specimens resemble *Orthocoelium streptocoelium* (Fischoeder, 1901), *O. scoliocoelium* var. *benoiti* (Grétillat, 1966) and *O. narayanai* (Gupta & Gupta, 1972) in having a pharynx of the paramphistomum type (*sensu* Näsmark, 1937). *Orthocoelium indonesiense* differs from *O. streptocoelium* in the absence of a posterior oesophageal sphincter, the presence of papillae on the wall of the genital atrium, the weakly developed genital sphincter and in having a long pars prostatica. It is distinguished from *O. scoliocoelium* var. *benoiti*, by the absence of an oesophageal bulb, by the presence of a sphincter papilla and of papillae on the wall of the genital atrium and by the weakly developed genital sphincter and from *O. narayanai* by the presence of a genital sphincter and by the long pars prostatica. *O. indonesiense* differs from all three in having a deep excretory vesicle and a different type of acetabulum. *O. streptocoelium* and *O. scoliocoelium* var. *benoiti* have acetabula of the streptocoelium type and *O. narayanai* has an acetabulum of the calicophoron type, whereas *O. indonesiense* has a gastrothylax-type acetabulum.

Näsmark (1937) referred the pharynx of *O. orthocoelium* (Fischoeder, 1901) to paramphistomum type, although Fischoeder (1903), in his original description, clearly stated that an anterior sphincter was present in the pharynx, and illustrated it. This feature is not found in a paramphistomum type pharynx. Re-examination of a series of sections labelled "*Ceylonocotyle orthocoelium*" from Näsmark's collection of amphistomes loaned from the Swedish Museum of Natural History revealed that an anterior sphincter, in the form of a roughly oval area of circular muscle bundles, is present in the pharynx about 0.082 mm from its anterior end. Lee & Lowe (1971) also observed an anterior sphincter in the pharynx of their Malayan specimens of *orthocoelium*, as has the present author specimens obtained from *Bubalus bubalis* and *Bos taurus* in the Philippines and China, respectively. Additional characters which differentiate *O. orthocoelium* from *O. indonesiense* are the presence of a long oesophagus, a short pars prostatica, straight caeca and a streptocoelium-type acetabulum.

Price & McIntosh (1953) tentatively moved *Cotylophoron okapi* Leiper, 1935 to the genus *Orthocoelium*, mainly because Laurer's canal does not cross the excretory vesicle or duct. The transfer was accepted by Yamaguti (1971) but re-examination of the type specimens showed that the species can neither be retained in the

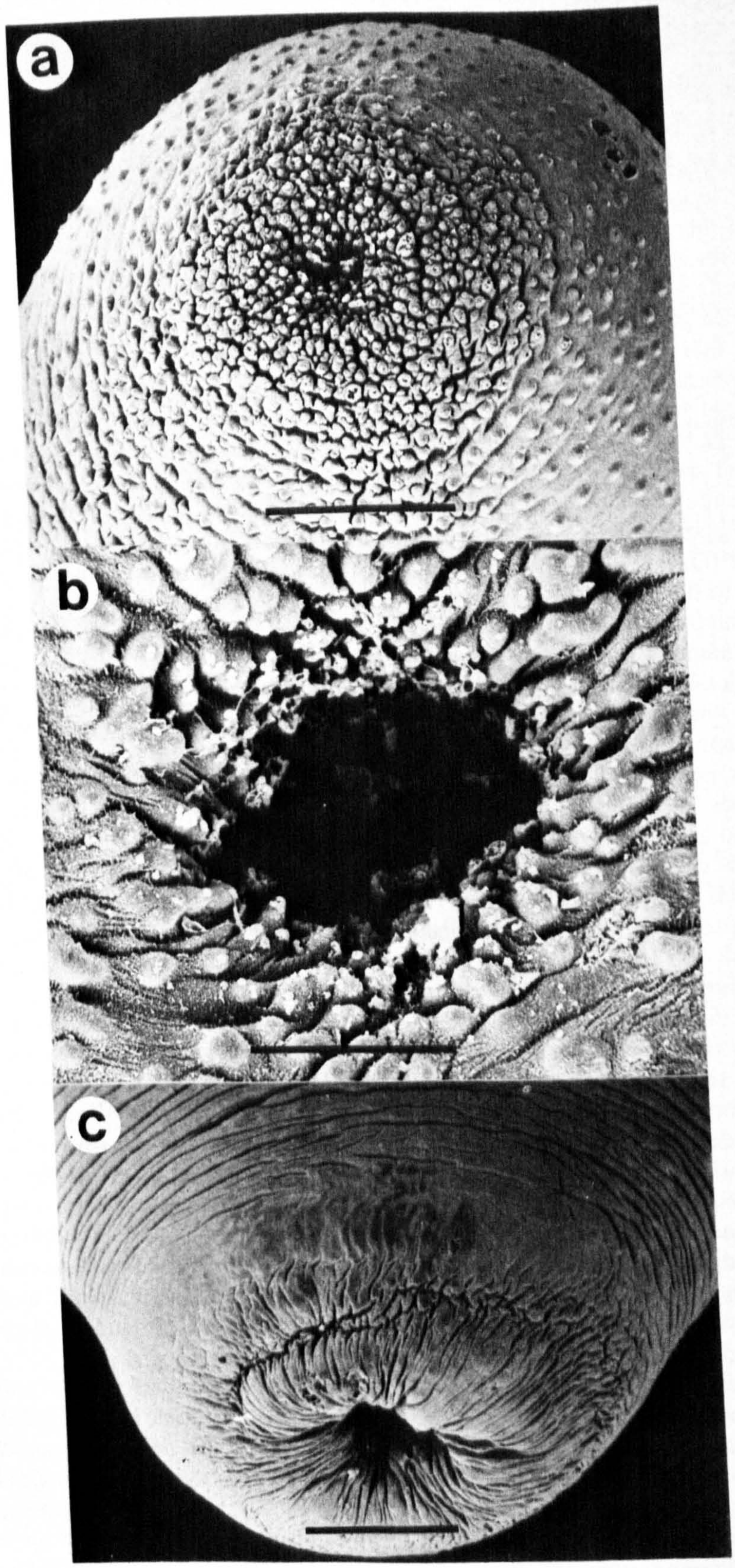


Plate I. *Orthocoelium indonesiense* n.sp.—SEM photomicrographs
a: Dome-like tegumental papillae on anterior end and around oral opening (bar—200 μm)
b: Genital pore surrounded by papillae (bar—20 μm)
c: Acetabular region, note absence of tegumental papilla (bar—300 μm)

genus *Cotylophoron* Stiles & Goldberger, 1910 because Laurer's canal does not cross the excretory vesicle or duct nor in the genus *Orthocoelium* because of the presence of a genital sucker. A paper in which the taxonomic position of *C. okapi* will be discussed in detail is in preparation.

Two species, *O. parvipapillatum* (Stiles & Goldberger, 1910) and *O. naesmarki* (Mukherjee, 1963), have pharynges, acetabula and genital atria of unknown types and *O. indonesiense* cannot, therefore, be compared with them on the bases of these structures. Nevertheless, the new form is readily distinguished from both by the long pars prostatica, the absence of an oesophageal bulb, the deep excretory vesicle and the limited extent of the caeca which do not reach the level of the acetabulum.

O. indonesiense differs from all the remaining species, namely, *O. dicranocoelium* (Fischoeder, 1901) *O. scoliocoelium* (Fischoeder, 1904), *O. dawesi* (Gupta, 1958) and *O. tamilensis* (Gupta & Bakhshi *in* Gupta & Nakhasi, 1977), in the absence of a lip sphincter in the pharynx and the gastrothylax type acetabulum. It differs further from *O. dicranocoelium* and *O. scoliocoelium* in the absence of an oesophageal bulb, from *O. dawesi* in the presence of a sphincter papilla and from *O. tamilensis* and *O. dicranocoelium* in the presence of a genital sphincter and sphincter papilla.

These differences are sufficient to justify the erection of a new species for which the name *Orthocoelium indonesiense* is proposed after the country of origin of the materials.

Hosts: *Bos indicus* (zebu) and *Ovis* sp. (sheep)
Habitat: rumen
Type locality: Yogyakarta Special Territory, Indonesia
Type specimens: Deposited in the Commonwealth Institute of Helminthology as type collection numbers S1036/B (holotype) and S1036/A (paratypes), and the British Museum (Natural History) as registration number 1979.9.11.1–3 (paratypes).

Acknowledgements

I am grateful to Dr. L. F. Khalil under whose guidance and supervision this study was undertaken, to Dr. Sheila Willmott for her interest in this study and to Dr. A. Andersson and Dr. R. Oleröd for the loan of Näsmark's specimens. I also wish to thank Dr. Wardiarto for providing specimens, Mrs. May Getley for technical assistance and Mrs. E. Gascoigne and Mrs. S. Eames for translating Russian and French references, respectively.

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Accepted for publication 10*th September*, 1979.

Orthocoelium dinniki n. sp.

TYPE SPECIMENS: Deposited in the Helminth Collection of the Commonwealth Institute of Helminthology, Type Coll. Nos. S1045/A (holotype), S1045/B (paratypes)

MATERIALS EXAMINED: Hosts, localities and donors/collections

Bubalus bubalis	Philippines	Author's own collection
Cattle	Shanghai, China	London School of Hygiene & Tropical Medicine
	Tokyo, Japan	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection
Goat	China	London School of Hygiene & Tropical Medicine

HABITAT: Rumen

DESCRIPTION:

Body conical, somewhat slightly flattened ventrally, 4.53-5.52 mm long, 1.81-2.18 mm in greatest width in the dorso-ventral direction. Body surface has dome-shaped papillae on the anterior end around the oral opening and ventrally on the wall ot the genital atrium.

Acetabulum subterminal, 1.o3-1.31 mm in external diameter in the dorso-ventral direction; ratio to body length 1:3.9 to 1:5.2; of the streptocoelium type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 12-18; d.i.c., 23-29; v.e.c., 10-15; v.i.c., 23-34; m.e.c., 4-12.

Pharynx 0.40-0.63 mm long, 0.40-0.60 mm in the dorso-ventral direction; ratio to body length 1:8.4 to 1:10, to the diameter of the acetabulum 1:1.7 to 1:2.4; of the calicophoron type (sensu Dinnik, 1964) in median sagittal section. Oesophagus 0.32-0.54 mm long, musculature of wall moderate in thickness but thickened in its posterior end to form a sphincter, lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form shallow dorso-ventral bends, reach level of acetabulum with the blind ends directed postero-ventrally.

Testes relatively large, lobed, tandem in posterior two third of the body; anterior testis 0.55-0.99 mm long, 0.87-1.59 mm in the dorso-ventral direction; posterior testis 0.58-1.09 mm long, 1.09-1.71 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa thick-walled, relatively well developed and convoluted; pars prostatica 0.21-0.30 mm long and 0.14-0.29 mm wide.

Ovary subspherical, 0.24-0.41 by 0.17-0.47 mm, posterior to testes and anterior or at level of the anterior border of acetabulum; Mehlis' gland close to ovary, 0.18-0.29 by 0.17-0.47 mm; uterus winds forward, dorsal to the testes then ventral to the male ducts; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface about 0.60-0.73 mm anteriorly to the excretory pore; vitellaria in lateral fields, extend from level of oesophagus to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 135-159 by 70-84 µm.

Genital pore opens on the ventral surface at level of the oesophagus or its bifurcation; of the papillogenitalis type (sensu Eduardo, 1980a) in median sagittal section.

Excretory vesicle dorsal to acetabulum, ovary and Mehlis' gland; excretory pore opens on the dorsal surface posteriorly to the Laurer's canal opening.

FIGURE 156

Orthocoelium dinniki n. sp.

(SEM)

a. Whole worm, ventral view (scale bar = 300 µm)

b. Anterior end, note papillae around the oral opening (scale bar = 100 µm)

c. Genital pore region, note papillae on the wall of the genital atrium (scale bar = 100 µm)

d. Acetabular region (scale bar = 100 µm)

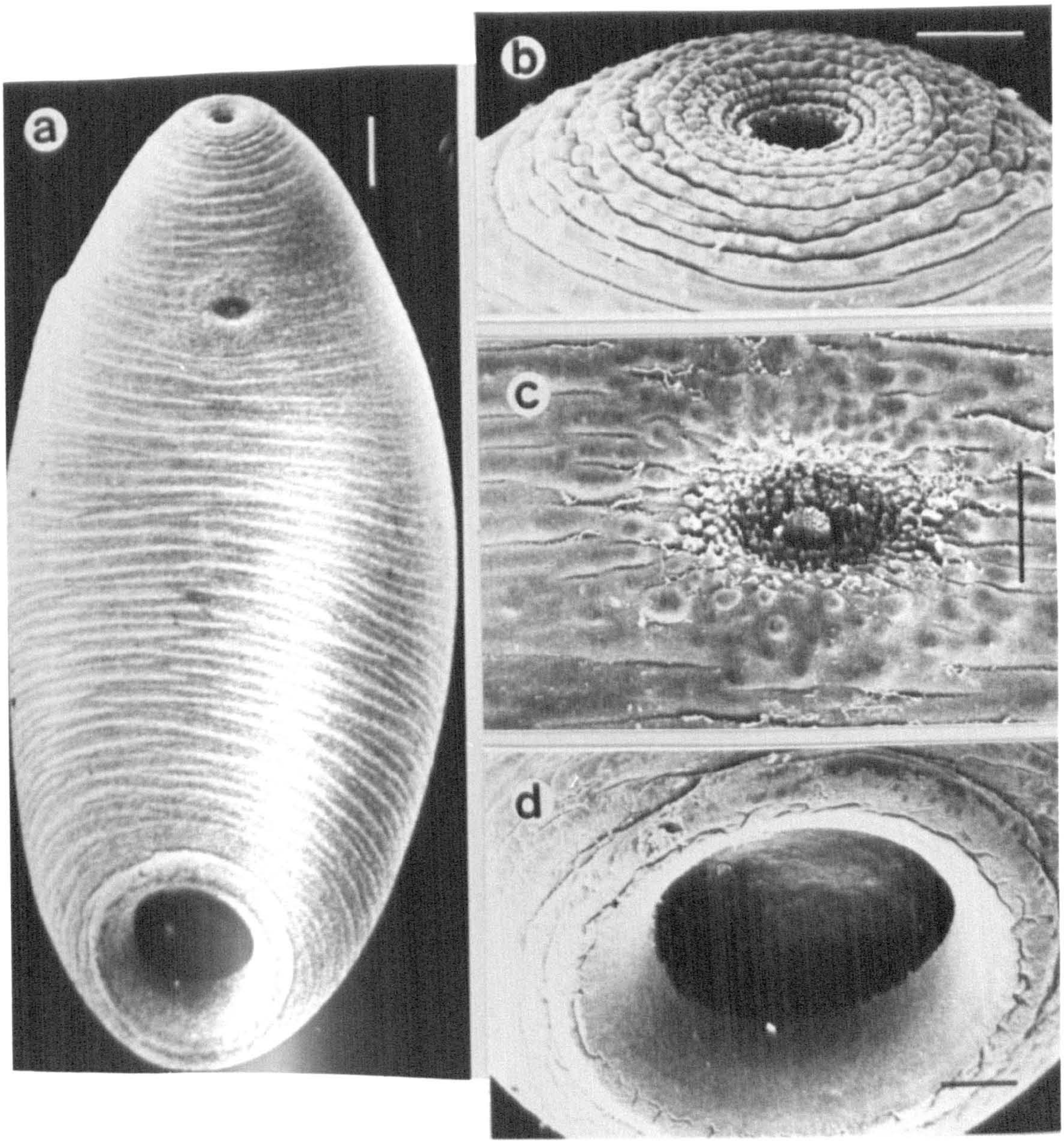

a
b
c
d

FIGURE 157

Orthocoelium dinniki n. sp.

a. Whole worm, ventral view

b. Whole worm, sagittal view

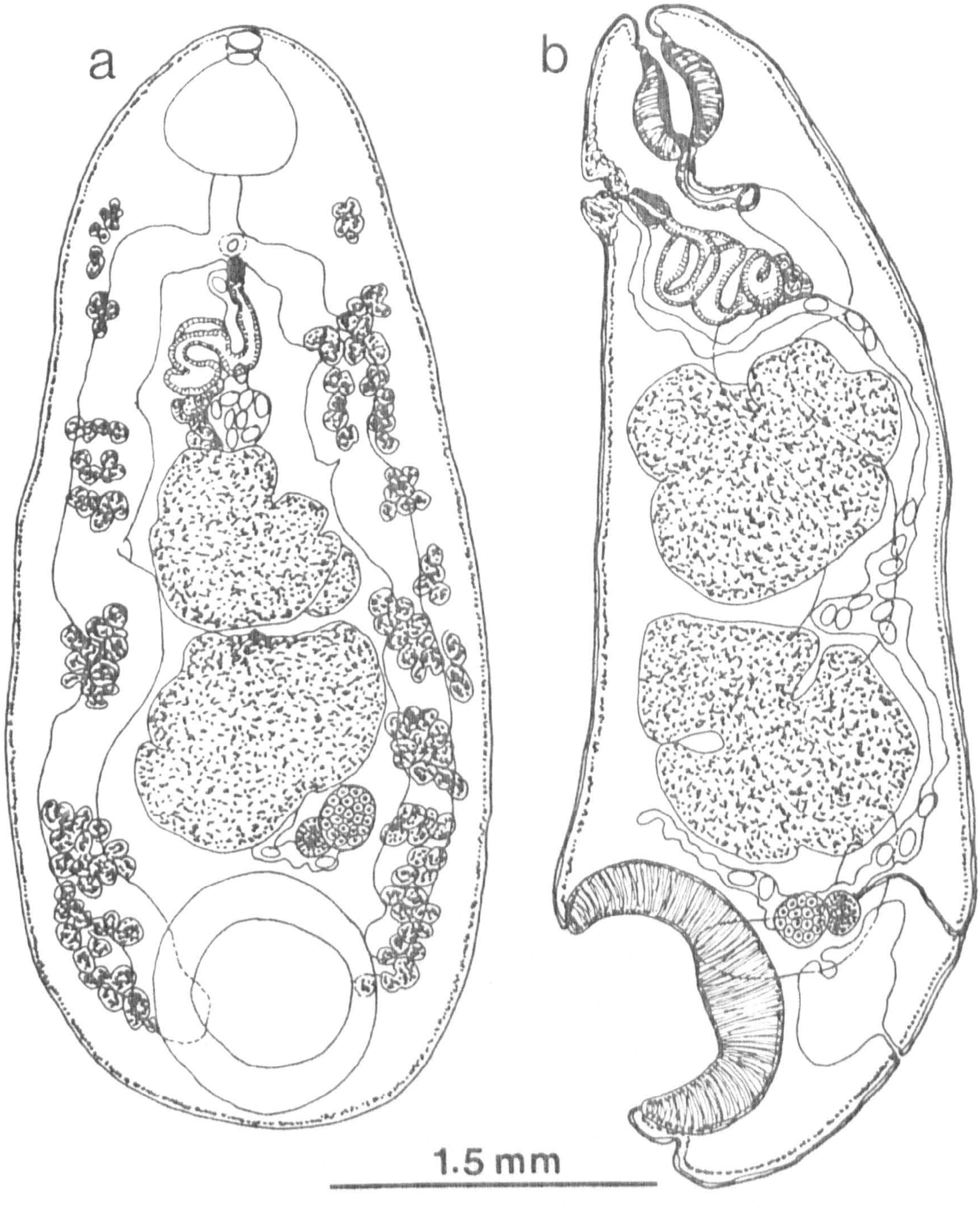

a
b
1.5 mm

FIGURE 158

Orthocoelium dinniki n. sp.

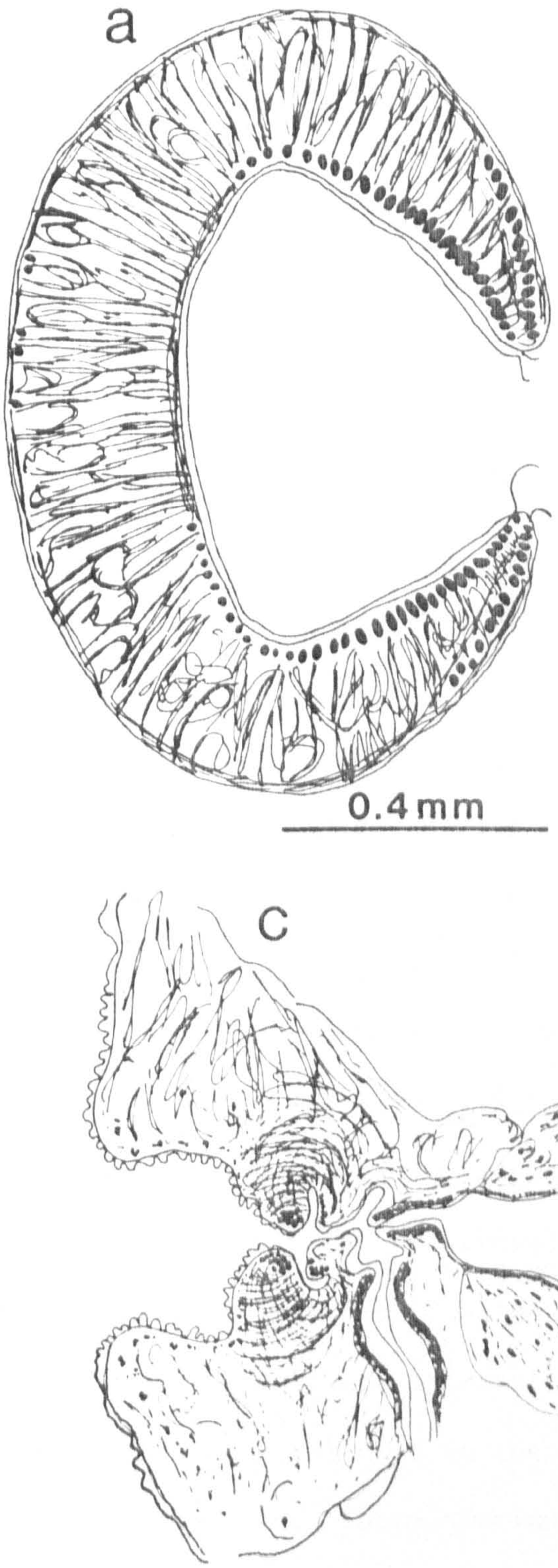
(median sagittal section)

a. Acetabulum (streptocoelium type)

b. Pharynx (calicophoron type) and oesophagus, note posterior sphincter of oesophagus.

c. Terminal genitalium (papillogenitalis type), retracted form and pars prostatica.

d. Another terminal genitalium (papillogenitalis type), relaxed form.


a
0.4mm
b
0.2mm
c
d
0.2mm
c,d

DISCUSSION

Price and McIntosh (1953) have already pointed out that the subgenus Orthocoelium Stiles and Goldberger, 1910 and the genus Ceylonocotyle Näsmark, 1937 are synonymous and that the former has priority over the latter because under the rules of the International Code for Zoological Nomenclature, subgenera have the same nomenclatural status as genera. Yamaguti (1971) recognised and accepted the synonymy and formally raised Orthocoelium to full generic rank. Consequently, he moved all species at that time described under Ceylonocotyle to the genus Orthocoelium. He however did not include Ceylonocotyle gigantopharynx Schad, Kuntz, Anteson and Webster, 1964. Instead, he moved the species to the genus Paramphistomum without giving any reason and even without having examined specimens of it. Ceylonocotyle gigantopharynx was established by Schad, Kuntz, Anteson and Webster (1964) as a new name for the specimens described and identified by Dawes (1936) and Tandon (1955b) as Paramphistomum gotoi. They found out that the specimens of the two above mentioned authors were not co-specific with Paramphistomum gotoi Fukui, 1922 and re-described Ceylonocotyle gigantopharynx based on specimens from buffloes in North Borneo, Malaysia. In this study, several specimens identical with Ceylonocotyle gigantopharynx from Bubalus bubalis in the Philippines were examined. The original material of Dawes (1936) identifed as Paramphistomum gotoi kept in the British Museum (Natural History) was also examined. These specimens together with the description and illustration of Dawes (1936) and Tandon (1955b) confirm the observations of Schad, Kuntz, Anteson and Webster (1964) and the justification of establishing their species. This species is

characterized by having a Laurer's canal which does not cross the excretory vesicle or duct and because of this it falls under the subfamily Orthocoeliinae. Schad, Kuntz, Anteson and Webster (1964) have rightly assigned the species under the genus Ceylonocotyle because the pars musculosa is relatively well developed and a genital sucker is absent. Since Ceylonocotyle is now a synonym of Orthocoelium, the species is here moved to the latter genus in a new combination. Yamaguti (1971) is unjustified in allocating the species to the genus Paramphistomum because this genus belongs to the subfamily Paramphistominae which is characterized by Laurer's canal crossing the excretory vesicle or duct. He himself has accepted this character as of value in the subfamily level and employed it in separating the Paramphistominae and the Orthocoeliinae. The specimens from Bubalus bubalis in Malaysia identified recently by Lee and Lowe (1971) as Paramphistomum gotoi were also re-examined in this study and found to be Orthocoelium gigantopharynx.

The validity of Orthocoelium parvipapillatum (Stiles and Goldberger, 1910) has been doubted by Näsmark (1937) who considered it to be either a synonym of Orthocoelium scoliocoelium or O. dicranocoelium but he was unable to re-examine the type specimens. The writer has re-examined the type specimens loaned from the United States National Parasite Collection, USDA, Beltsville, Maryland and also examined new materials of this species from Indonesia. As shown in the redescription of the species provided here and in the key to the species of the genus given below, the species in question is distinct and valid and is separable from the rest of the species in the genus. Näsmark (1937) was in error in referring the terminal

genitalium of Orthocoelium orthocoelium to the gracile type. Re-examination of the type specimens and also examination of new specimens of the species from various hosts and localities in Asia revealed that its terminal genitalium is not of the gracile type but of a new type, the orthocoelium type which is already defined earlier in this work.

Stiles and Goldberger (1910) described Paramphistomum shipleyi as a new species from Cervus eldi but the locality is unknown. Maplestone (1923) regarded it as a synonym of Orthocoelium orthocoelium while Näsmark (1937) considered it a synonym of O. scoliocoelium. The type specimens could not be traced but it is clear from the original description and illustration that the species as earlier pointed out by Näsmark (1937) is a junior synonym of Orthocoelium scoliocoelium.

Tandon (1955a) described Paramphistomum spinicephalus from the rumen of Bubalus bubalis in Lucknow, India. Mukherjee and Chauhan (1965) listed it under the genus Ceylonocotyle (now Orthocoeclium) and cited Mukherjee (1960) as the author who transfered the species to that genus. Yamaguti (1971) however listed it under the genus Paramphistomum with a note "generic status sub judice". The type specimens were re-examined loaned from the Zoological Survey of India (Reg. No. W5593/1, W5594/1, W5595/1). From the type specimens and the original description and illustration, the species in question belongs to the genus Orthocoelium because Laurer's canal does not cross the excretory vesicle or duct, a genital sucker is absent and the pars musculosa is relatively well developed and the species is identical in all respects with Orthocoelium orthocoelium and should be synonymized with it.

Grétillat (1966) described Ceylonocotyle scoliocoelium var. benoiti as a new variety from Syncerus caffer in Central Africa. Re-examination of the type specimens loaned from the Musée Royal de l'Afrique Centrale, Tervuren revealed that the species is not at all related to Ceylonocotyle (now Orthocoelium) scoliocoelium and does not belong to that genus. It is in fact a valid and independent species and belongs to the genus Leiperocotyle Eduardo, 1980. The species is therefore discussed in detail under the latter genus.

Gupta and Bakhshi (in Gupta and Nakhasi, 1977b) recently described Ceylonocotyle tamilensis as a new species from the stomach of cattle in Madras, India. The species was not differentiated from any member of the genus. Eduardo (1980b) moved it to the genus Orthocoelium in a new combination. The deposition of the type specimens was not indicated in the paper and several requests made to the authors for the loan of the types and other specimens have been unsuccessful. It is however evident from the available description and illustration that no distinct difference exists between this species and Orthocoelium dicranocoelium and therefore it is regarded here a junior synonym of the latter species.

Ceylonocotyle naesmarki was described by Mukherjee (1963) as a new species based on only two specimens recovered from the rumen of sheep in India. No sections were prepared and the specimens were flattened for examination. Yamaguti (1971) listed the species under Orthocoelium in a new combination. The types and other specimens are not available for examination. It is apparent however from the available description and illustration that the species is very

closely related to both Orthocoelium dicranocoelium and O. scoliocoelium but information on the histology of the pharynx, acetabulum and terminal genitalium is lacking and therefore the species can not be compared with the two above mentioned species on this basis. Because of this, it is very difficult to determine accurately its specific status. Until the types and other specimens are available for examination, the species in question is regarded here as species inquirenda.

The writer (Eduardo, 1980b) has recently described a new species of Orthocoelium, O. indonesiense and the published description is here appended. The pharynx was referred to the paramphistomum type (sensu Näsmark, 1937) but this type as already explained elsewhere in this work should now be referred to the calicophoron type (sensu Dinnik, 1964). Accordingly, the pharynx of O. indonesiense should now be referred correctly as of the calicophoron type.

The new species, Orthocoelium dinniki is assigned to the genus because Laurer's canal does not cross the excretory vesicle or duct, a genital sucker is absent and the pars musculosa is well developed. It resembles O. streptocoelium and O. gigantopharynx because of the presence of a posterior oesophageal sphincter but differs from both by the presence of tegumental papillae on the wall of the genital fold and further from the former species by the less developed genital sphincter and sphincter papilla which are not connected to each other; from the latter species by the caeca which do not cross the dorso-median line to opposite sides and by having a different type of pharynx. It resembles O. parvipapillatum and O. indonesiense because of the presence of tegumental papillae

on the wall of the genital fold but differs from the former by the absence of a lip sphincter in the pharynx, absence of an oesophageal bulb and the presence of both genital sphincter and sphincter papilla; from the latter by having a different type of acetabulum and absence of a posterior oesophageal sphincter.

The new species differs from O. orthocoelium and O. bovini by the absence of an anterior sphincter in the pharynx and the presence of tegumental papillae on the wall of the genital fold. It differs further from the former by having wavy caeca and a different type of acetabulum. It also differs from O. dicranocoelium, O. scoliocoelium and O. dawesi by the absence of a lip sphincter in the pharynx, absence of an oesophageal bulb and presence of tegumental papillae on the wall of the genital fold. It differs further from the first by the presence of both genital sphincter and sphincter papilla and from the last by the presence of a sphincter papilla. The new species is named after Dr. J.A. Dinnik whose works have contributed to the better understanding of the African amphistomes and whose enormous collection of amphistomes forms the bulk of materials for the present study.

A key to separate the species of the genus is provided below.

Key to the species of the genus Orthocoelium (Stiles and Goldberger, 1910) Price and McIntosh, 1953

1. Each caecum crosses the dorso-median line in its posterior part to the opposite lateral side; internal surface of pharynx with long papillae - - - - - O. gigantopharynx

   Caeca do not cross the dorso-median line; internal surface of pharynx lacks long papillae - - - - - - - - - - 2

2. Anterior pharyngeal sphincter present - - - - - - - - - - - - - 3

   Anterior pharyngeal sphincter absent - - - - - - - - - - - - - 4

3. Oesophagus long, with a posterior sphincter; caeca straight - - - - - - - - - - - - - - - O. orthocoelium

   Oesophagus short, lacks a posterior sphincter; caeca form coils - - - - - - - - - - - - - - - - - O. bovini

4. Lip sphincter of pharynx and oesophageal bulb present - - - 5

   Lip sphincter of pharynx and oesophageal bulb absent - - - - 7

5. Genital sphincter and sphincter papilla present; radial musculature fairly strong - - - - - - - - O. scoliocoelium

   Genital sphincter present; sphincter papilla absent; radial musculature fairly strong - - - - - - - - O. dawesi

   Genital sphincter and sphincter papilla absent; radial musculature weak - - - - - - - - - - - - - - - - - - 6

6. Genital fold with tegumental papillae - - - O. parvipapillatum

   Genital fold lacks tegumental papillae - - - O. dicranocoelium

7. Posterior oesophageal sphincter present - - - - - - - - - - - 8

   Posterior oesophageal sphincter absent - - - - - - - - - - - - 9

8. Genital sphincter and sphincter papilla well developed, the latter being extensive and connected to the former; genital fold lacks tegumental papillae - - - - - - - - - - - O. streptocoelium

   Genital sphincter and sphincter papilla not well developed, not extensive and not connected to each other; genital fold with tegumental papillae - - - - - - - - - - - - - - - - - O. dinniki n. sp.

9. Pars prostatica long; genital sphincter and sphincter papilla present; genital fold with tegumental papillae; excretory vesicle deep in the dorso-ventral direction - - - - - - - - - - - - - O. indonesiense

   Pars prostatica short; genital sphincter present; sphincter papilla absent; genital fold lacks tegumental papillae; excretory vesicle not deep in the dorso-ventral direction - - - - - - - - - O. narayanai

SYSTEMATIC PARASITOLOGY, 1 (2), 141–149 (1980).

BILATORCHIS PAPILLOGENITALIS N.G., N.SP. (PARAMPHISTOMIDAE: ORTHOCOELINAE), A PARASITE OF THE RED LECHWE (*KOBUS LECHE* GRAY, 1850) FROM ZAMBIA

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Summary

Bilatorchis papillogenitalis n.g., n.sp. from the red lechwe, *Kobus leche* Gray, 1850, from Zambia is described and illustrated. It is assigned to the subfamily Orthocoelinae Price & McIntosh, 1953 and distinguished from other members of the subfamily by the lateral and symmetrical position of the testes in the posterior third of the body between the caecal ends and the acetabulum, the intertesticular position of the ovary and Mehlis' gland and the limited extent of the caeca which end only at the level of the anterior border of the testes. A new type of genital atrium, papillogenitalis type is proposed for *B. papillogenitalis*, *Calicophoron papillosum*, *Carmyerius parvipapillatus* and, possibly, *Orthocoelium parvipapillatum*. The genus *Cochinocotyle* Gupta & Gupta, 1970 is moved to the subfamily Orthocoelinae.

Introduction

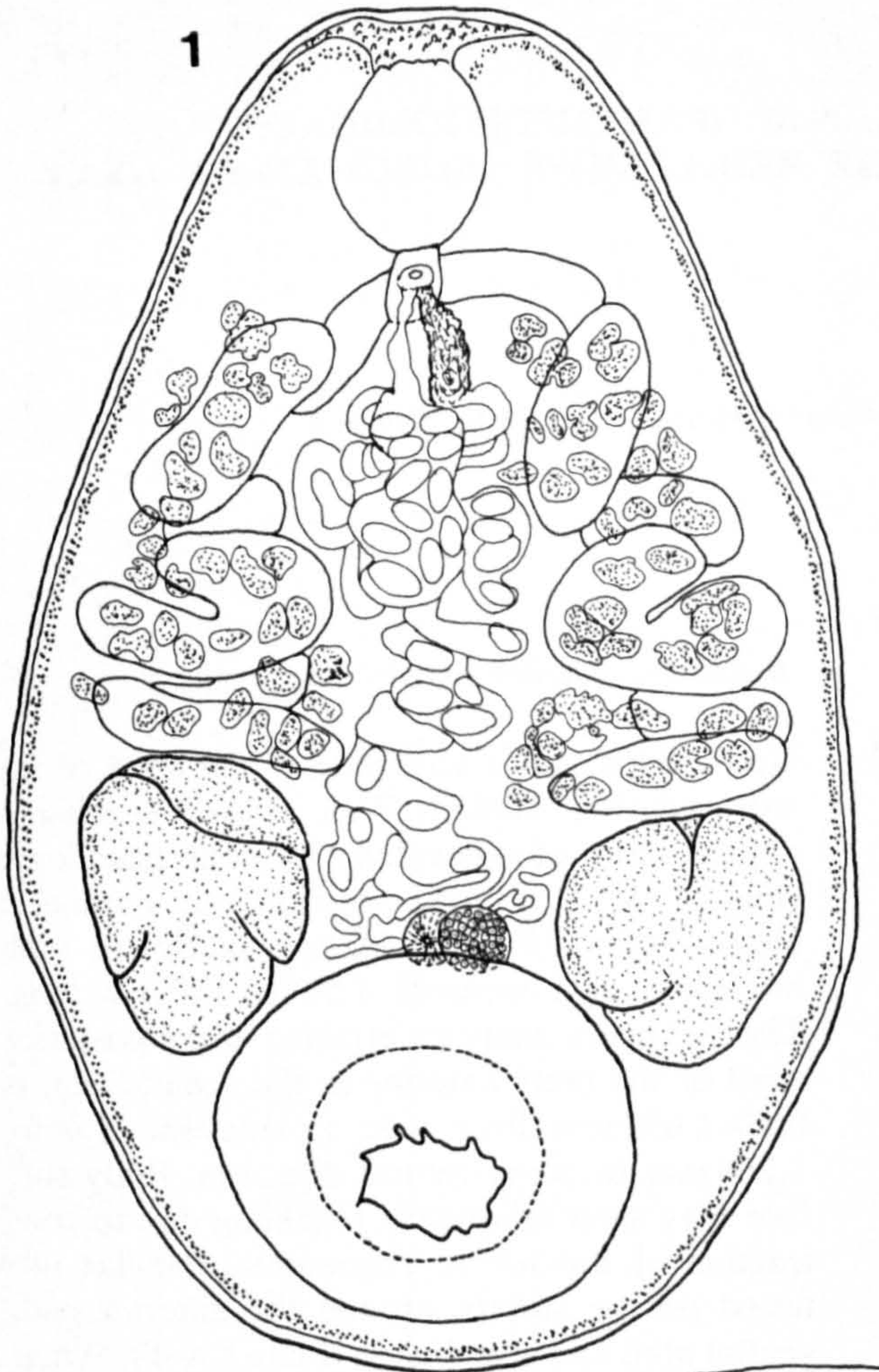
Examination of some unidentified paramphistomids in the helminthological collection of the London School of Hygiene & Tropical Medicine, now housed in the Commonwealth Institute of Helminthology, revealed the presence of an undescribed species. The material was collected by the late Dr. P.L. LeRoux and consisted of numerous specimens from the rumen of *Kobus leche* Gray, 1850 from Zambia. These were studied as stained whole mounts, thick hand sections and microscopic paraffin sections. Representative specimens were studied by the scanning electron microscope for surface topography.

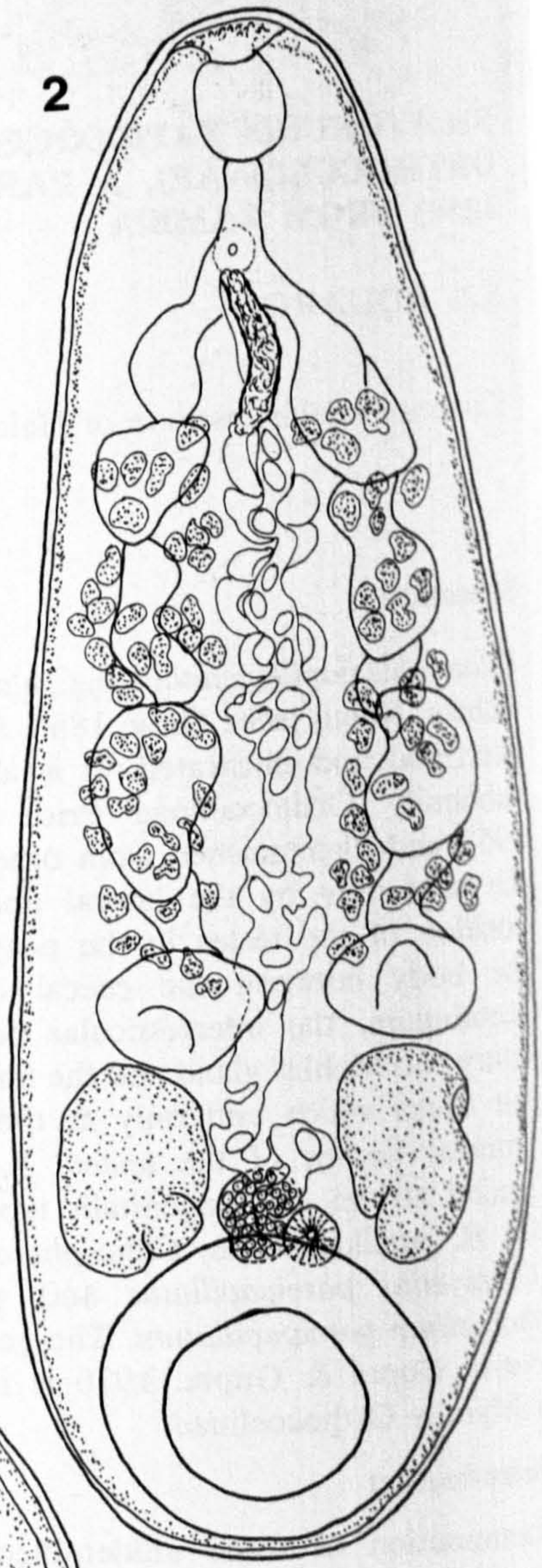
*Supported by a scholarship grant under the 4th Education Project of the Philippines with the World Bank.

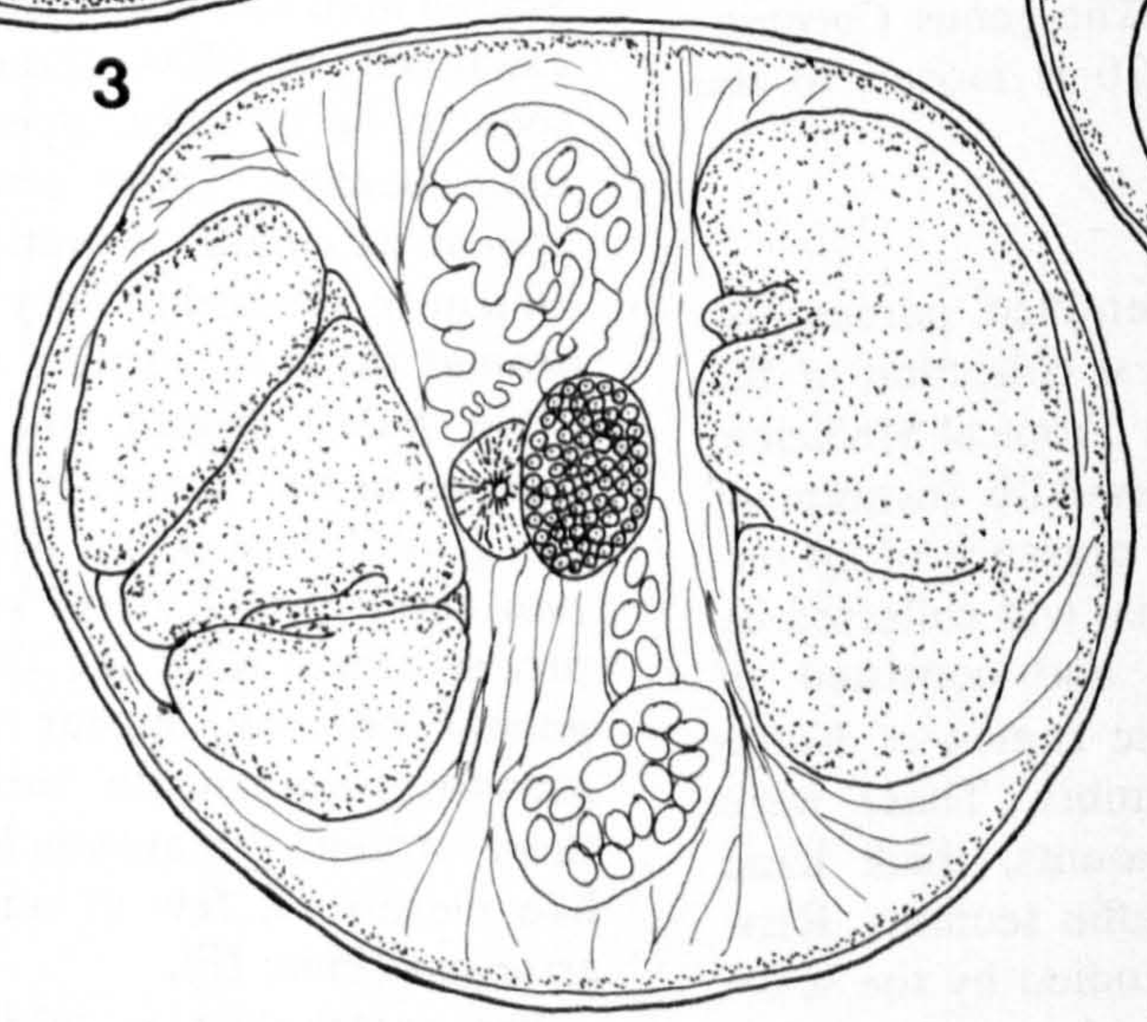
Bilatorchis papillogenitalis n.g., n.sp.

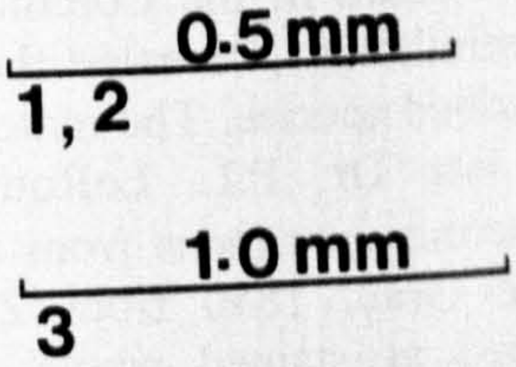
Body shape varies according to the state of the worm during fixation. Well relaxed specimens appear more elongate than do contracted ones (Figs. 1 & 2). In cross section, the outline is almost round (Fig. 3). Mature specimens with numerous eggs measure 1.508–4.160 mm long. The maximum diameter attained at the posterior third of the body anterior to the acetabulum, is 0.70–1.659 mm from side to side and 1.066–1.264 mm in dorso-ventral direction. Body surface may show transverse wrinkling due to contraction of the worm. Tegumental papillae are found on the surface around the anterior end, genital pore and acetabulum (Plate I A–F). When examined by SEM, these surface papillae are seen to be of three types which correspond to their location. Those around the anterior end appear as circular elevations, each about 10 to 20 μm in diameter. They form concentric rings around the oral opening and gradually become more widely spaced and more irregularly distributed as they extend posteriorly to the level of the genital pore (Plate IB), Each circular elevation has 14 to 22 apical knob-like projection or process (Plate IC & D). The papillae around the genital opening appear as club-shaped outgrowths with smooth surfaces (Plate IE) and those around the acetabulum are small, dome-like elevations, few in number and irregularly arranged (Plate IF).

The acetabulum is subterminal. Its external diameter, measured dorso-ventrally, is 0.61–0.79 mm and its ratio to the length of the body is







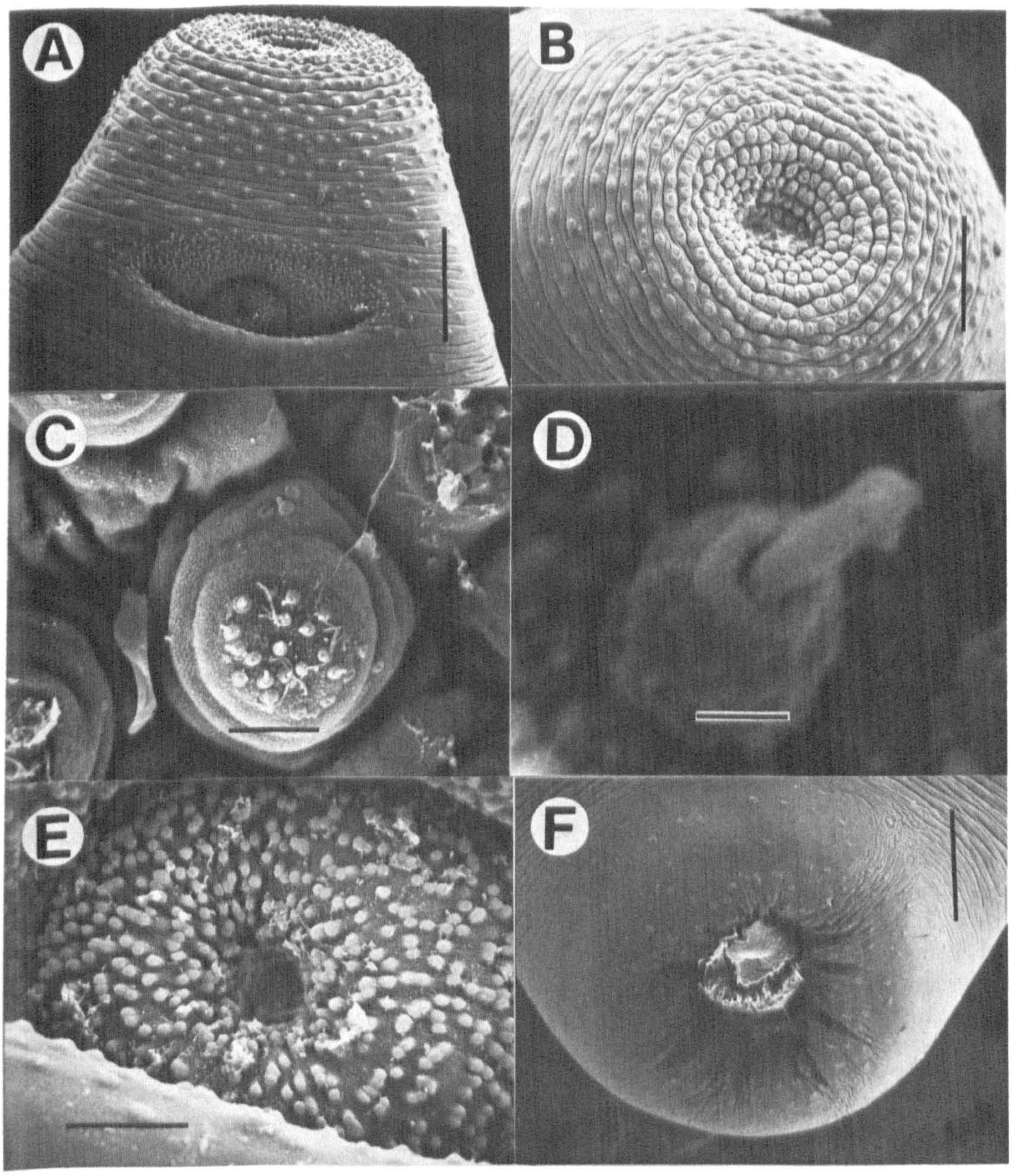


Bilatorchis papillogenitalis n.g., n.sp.

Fig. 1. Whole worm, ventral view

Fig. 2. Whole worm, well relaxed specimen, ventral view

Fig. 3. Cross section at level of tests, ovary and Mehlis' gland



Bilatorchis papillogenitalis n.g., n.sp.

Plate I A–F

A Surface of anterior half. SEM (bar = 200 μm)
B Circular elevations forming concentric rings around oral opening, SEM (bar = 200 μm)
C One circular elevation showing knob-like structures with processes, SEM (bar = 6 μm)
D Knob-like structure with process at higher magnification, SEM (bar = 1 μm)
E Genital atrium showing club-shaped papillae, SEM (bar = 30 μm)
F Acetabulum showing small papillae irregularly distributed around opening, SEM (bar = 200 μm)

1:2 to 1:4.8. In median sagittal section (Fig. 7), conforms to the nilocotyle type of acetabulum defined by Näsmark (1937) in that the dorsal exterior circular muscle series is not divided into two parts and the units of the external and internal series are almost equal in number. Few

circular muscle units are found in the dome. The circular muscle units of the interior series are larger in the middle than at either end of the series. Radial muscle fibres are well developed. The number of circular muscle units is as follows: dorsal exterior, 30 to 34; dorsal interior, 30 to 32; ventral interior, 31 to 35; ventral exterior, 30 to 32 and dome, four to eight.

The pharynx is 0.102–0.265 mm long and 0.081–0.096 mm in width, dorso-ventrally. Its ratio to the length of the body is 1:8 to 1:15 and to the diameter of the acetabulum is 1:2 to 1:3.05. In median sagittal section, it agrees with the paramphistomum type of pharynx described by Näsmark (1937), although a few weakly developed, middle circular muscle units can be seen (Fig. 8). There are no muscular sphincters (lip, anterior or posterior) or diverticula.

The oesophagus is 0.206–0.294 mm long and has no muscular bulbous expansion. It bends slightly dorsally from the point of origin of the caeca. The internal surface lining is the same as that of the body surface. The caeca run posteriorly down the lateral sides of the body, making four dorso-ventral bends, and terminate at the posterior border of the middle third of the body either just in front of the testes or at the level of their anterior borders. In no specimen did the caeca extend beyond the anterior borders of the testes. The blind ends are always directed ventrad. The tightness of the bends depends on the state of contraction of the body (Figs. 5 & 6).

The testes, which are lobed and almost equal in size, lie laterally and symmetrically in the posterior third of the body between the ends of the caeca and the antero-lateral border of the acetabulum (Figs. 1, 2 & 3). The testes measure 0.294–0.566 mm antero-posteriorly and 0.66–1.174 mm dorso-ventrally and, in sagittal section, they appear dorso-ventrally elongated with well defined lobes. The pars prostatica is long (0.324–0.485 mm), almost straight and is about three or four times as long as it is wide. The pars musculosa is well developed and tightly coiled and the thin-walled vesicula seminalis lies posterior to it.

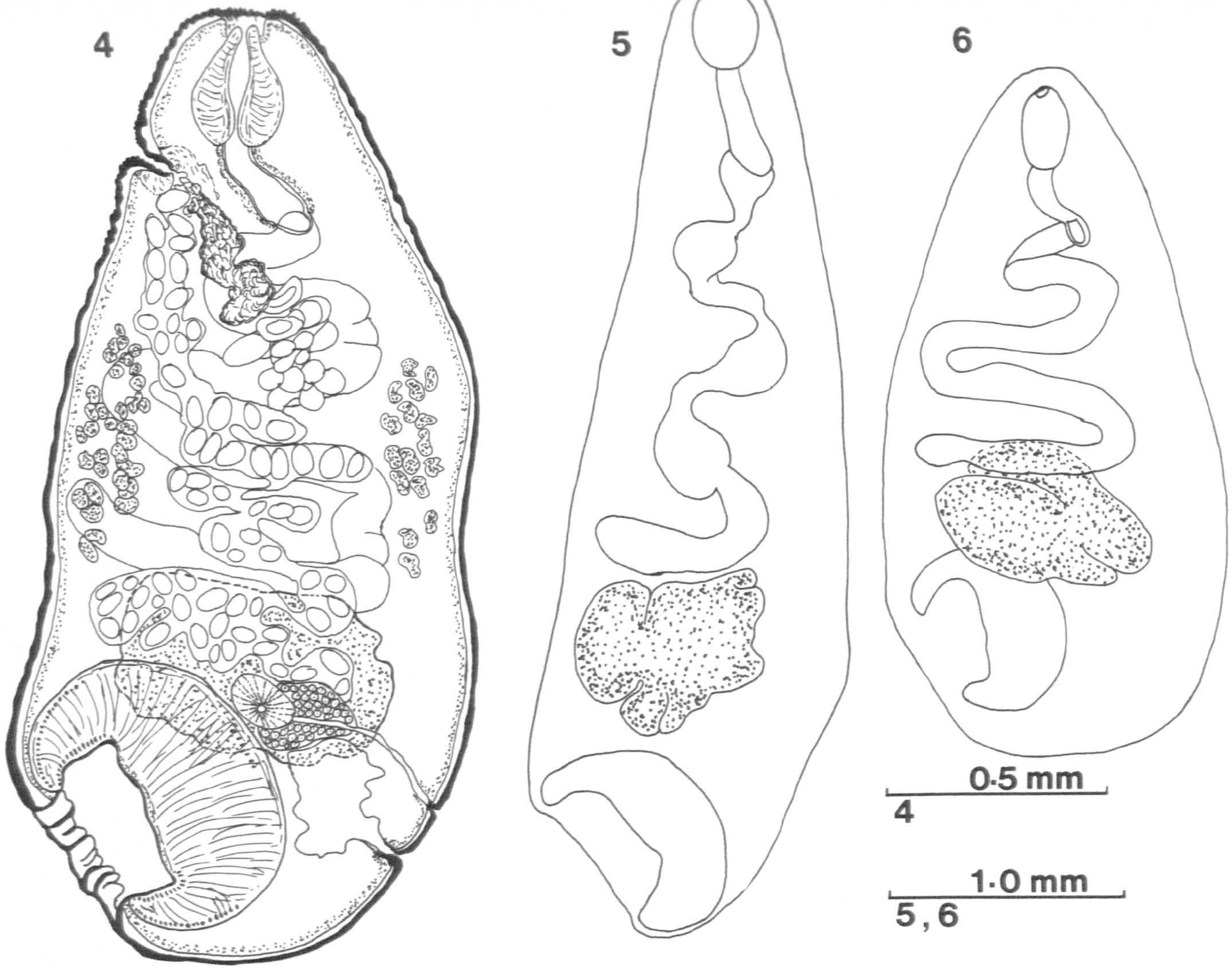
The ovary is oval or spherical in outline and lies medially between the testes, dorsal to the acetabulum and anterior to the excretory vesicle (Figs. 3 & 4). It measures 0.088–0.388 mm antero-posteriorly and 0.177–0.201 mm dorso-ventrally. The spherical Mehlis' gland, which lies close to but slightly ventrally to the ovary, measures 0.188–0.236 mm by 0.147–0.206 mm. Laurer's canal emerges from the dorsal side of Mehlis' gland, runs anterior to the excretory vesicle and opens dorsally anterior to the excretory pore (Fig. 4). The coiled uterus runs between the testes initially, between the caeca anteriorly and ventrally to the male ducts in its distal part. The eggs are oval, operculate and measure 10.51–12.98 by 5.90–6.75 μm. Clusters of vitelline glands extend laterally from the oesophageal bifurcation to the anterior border of the testes.

The excretory vesicle lies dorsally to the acetabulum and its duct opens posteriorly to the opening of the Laurer's canal.

The genital opening lies ventrally at the level of the oesophagus about 0.385–0.800 mm from the anterior end. In all specimens examined, the genital papilla lies at the bottom of an atrium whose wall is lined by small club-shaped papillae which extend for a very short distance over the outside surface around the opening (Plate Ia). A distinct circular fold surrounds the genital papilla and its external surface is also lined by papillae of the same type. In median sagittal section (Fig. 9), the circular fold shows a genital sphincter which consists of few weak circular muscle units but has well developed radial fibres. The genital papilla is of moderate size and the sphincter in its basal part is poorly developed and sometimes indistinct.

Discussion

The subfamily Orthocoelinae was proposed by Price & McIntosh (1953) for those genera of the family Paramphistomidae Fischoeder, 1901 *sensu stricto* in which the Laurer's canal does not cross the excretory vesicle or duct, the body is not divided into two parts and pharyngeal pouches are absent. Yamaguti (1971) accepted the subfamily and included in it the following genera: *Orthocoelium* (Stiles & Goldberger, 1910) Yamaguti, 1971; *Buxifrons* (Fukui, 1929) Näsmark, 1937; *Nilocotyle* Näsmark, 1937;

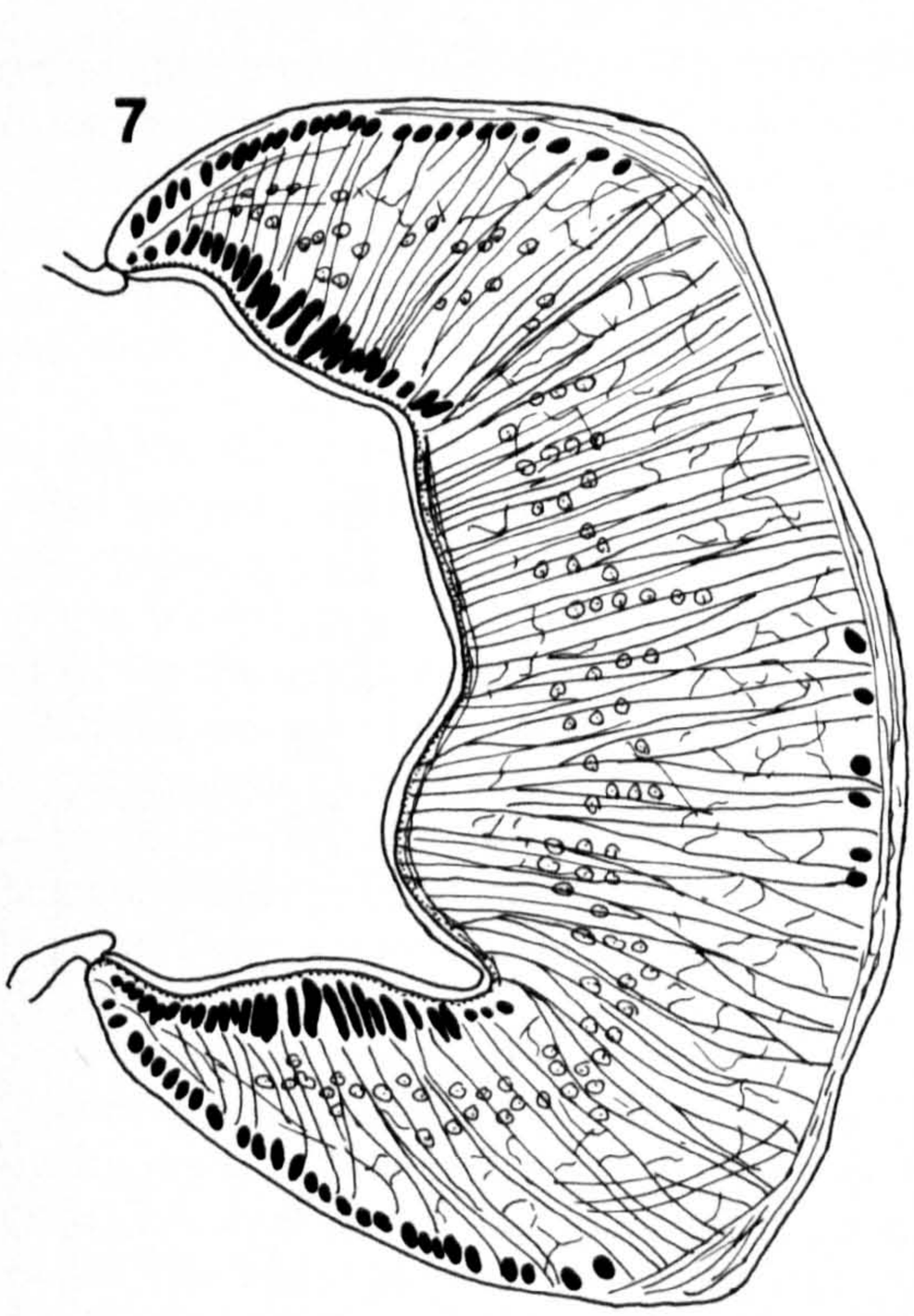


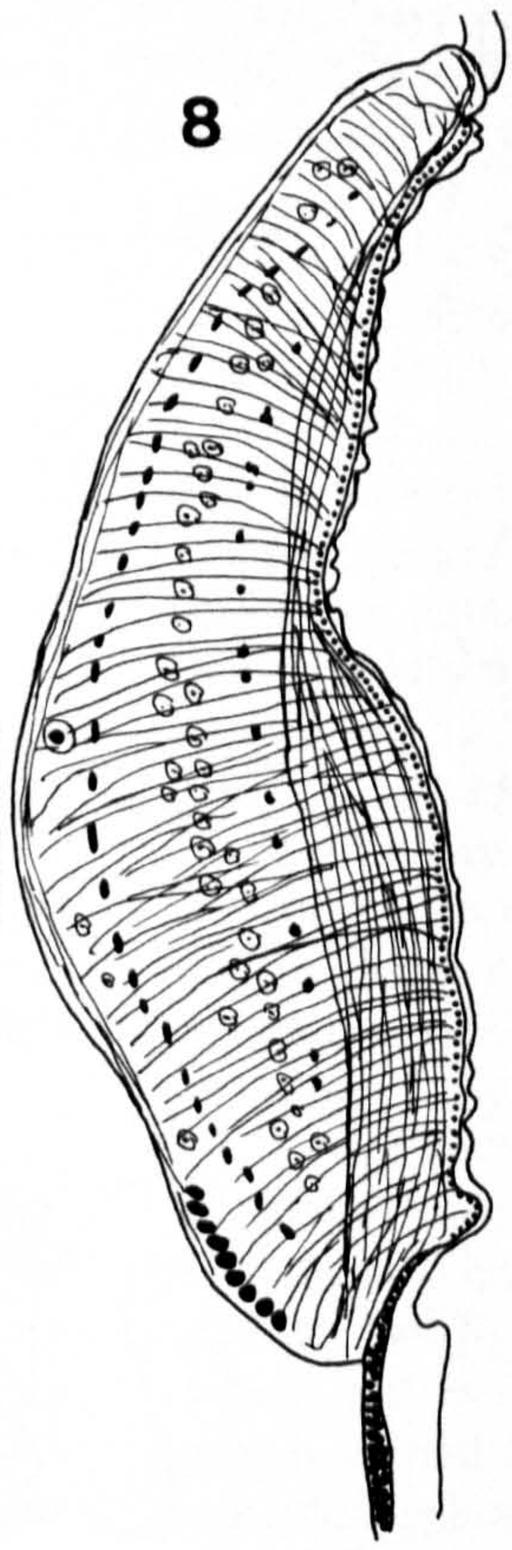
Bilatorchis papillogenitalis n.g., n.sp.

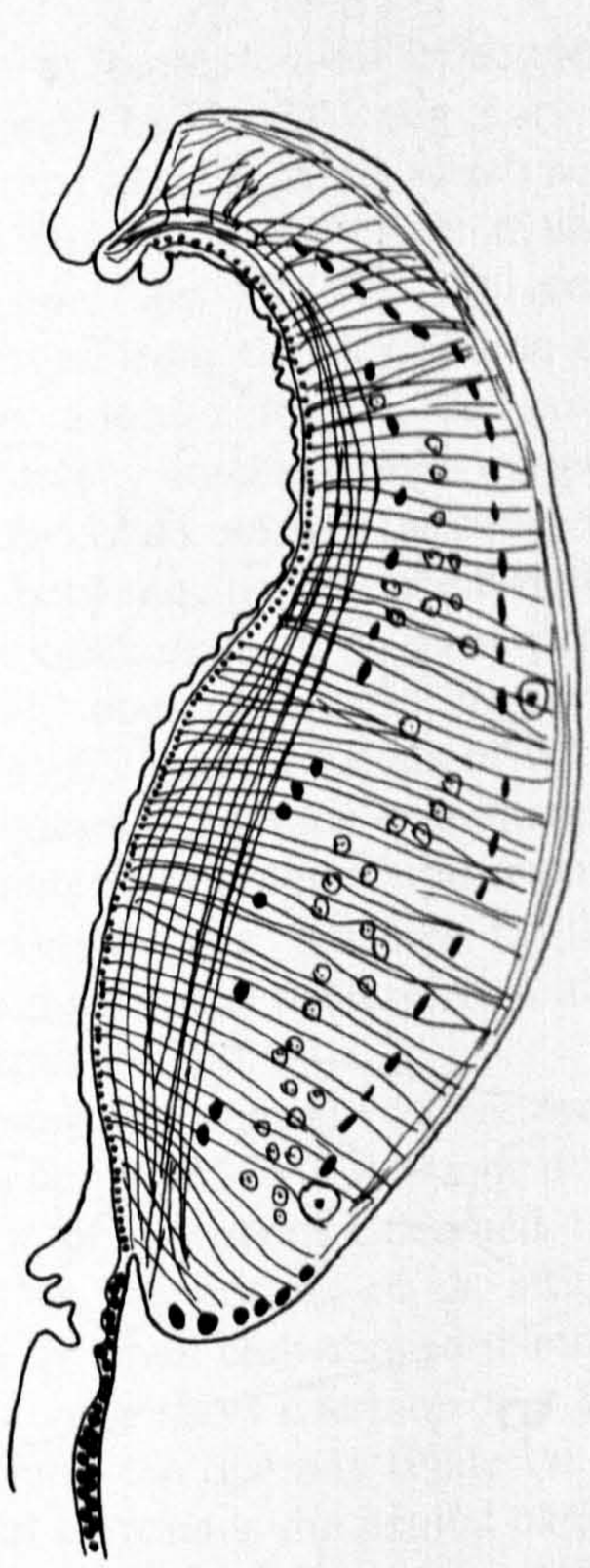
Fig. 4. Whole worm, sagittal view

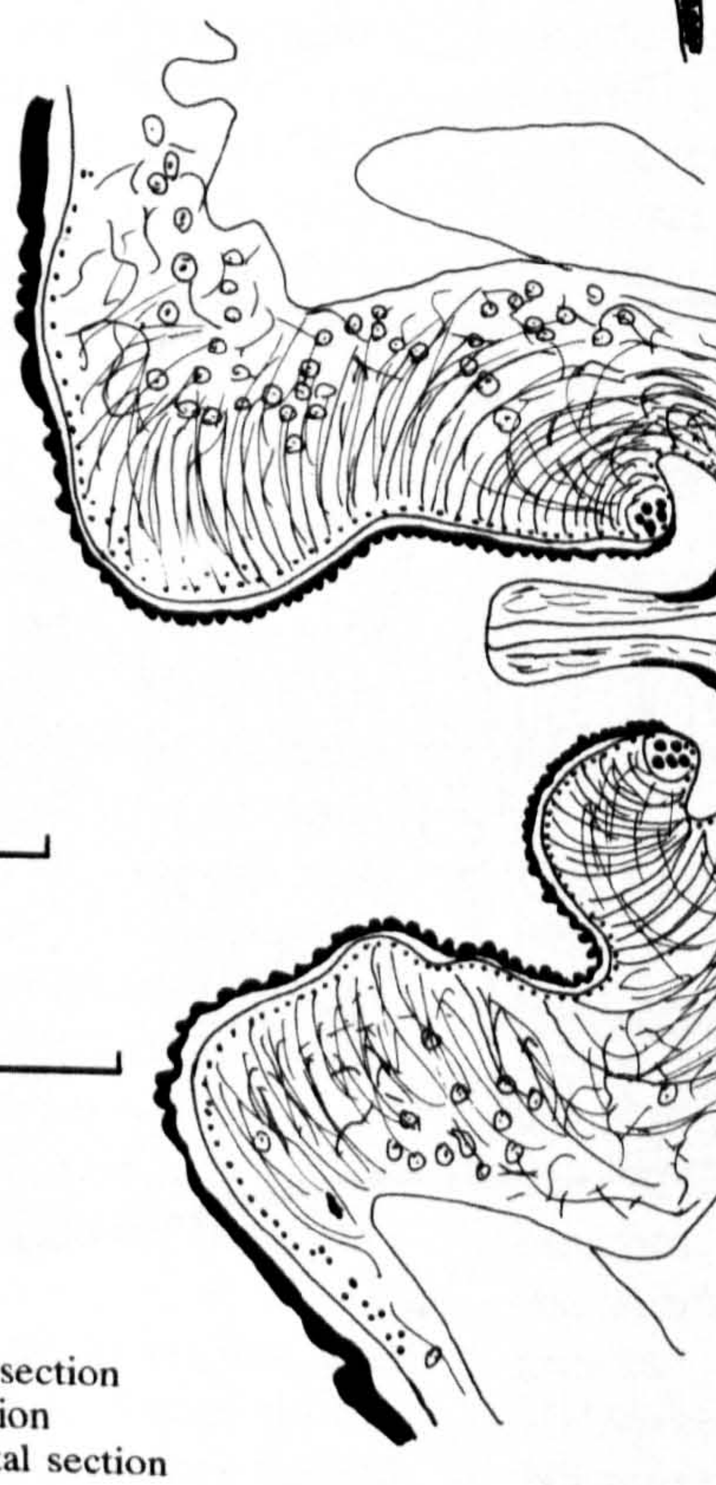
Fig. 5. Caecum of well relaxed specimen showing dorso-ventral bends

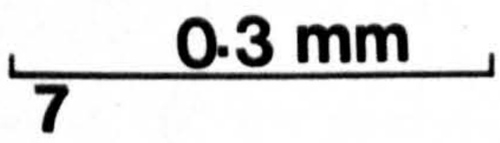
Fig. 6. Caecum of contracted specimen showing dorso-ventral bends

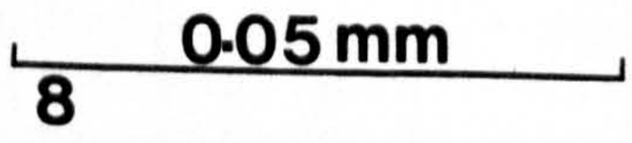


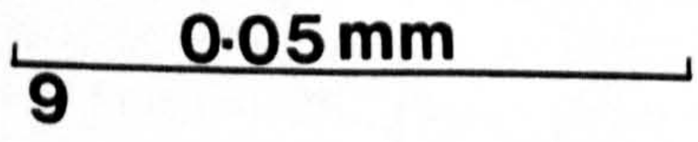












Bilatorchis papillogenitalis n.g., n.sp.

Fig. 7. Acetabulum, median sagittal section
Fig. 8. Pharynx, median sagittal section
Fig. 9. Genital atrium, median sagittal section

Macropharynx Näsmark, 1937; *Gigantoatrium* Yamaguti, 1958; *Glyptamphistoma* Yamaguti, 1958; *Paramphistomoides* Yamaguti, 1958; *Platyamphistoma* Yamaguti, 1958; and *Pseudoparamphistoma* Yamaguti, 1958. Gupta & Gupta (1970) (the paper did not appear until late 1971) described *Cochinocotyle bovini* from cattle in India as representing a new genus and new species. Although *Cochinocotyle* has the features of the subfamily Orthocoelinae, it was assigned to the subfamily Paramphistominae Fischoeder, 1901, the authors apparently being unaware of Price & McIntosh's paper. They must, however, have realized the importance of the crossing between Laurer's canal and the excretory vesicle or duct since they subdivided members of the subfamily Paramphistominae into groups based on this feature, placing their genus among those in which Laurer's canal does not cross the excretory vesicle or duct. The genus *Cochinocotyle* should, therefore, be moved to the subfamily Orthocoelinae. The genera in this subfamily can be differentiated from each other by a combination of characters including the shape of the body, the development of the pars musculosa, the size of the genital atrium and genital papilla and the extent of the vitellaria.

Bilatorchis papillogenitalis belongs to the subfamily Orthocoelinae because Laurer's canal does not cross the excretory vesicle, the body is not divided into two parts, there are no pharyngeal diverticula and there is no ventral pouch. Nevertheless, it cannot be assigned to any of the genera mentioned above and can be differentiated from all of them. The well-developed pars musculosa in the present species resembles those of the genera *Orthocoelium* and *Cochinocotyle* but the new form differs from both and from *Buxifrons* in having a nilocotyle type acetabulum. It differs further from *Cochinocotyle*, which has so far been reported only from *Hyelaphus porcinus* in India, in possessing a paramphistomum type pharynx.

In possessing a nilocotyle type of acetabulum, *Bilatorchis* resembles *Nilocotyle*, *Gigantoatrium*, *Glyptamphistoma* and *Platyamphistoma* but differs from all these and from *Paramphistomoides* in having a long, well-developed pars musculosa and pars prostatica. It differs further from *Glyptamphistoma* in the absence of parallel hoops on the surface of the body and from *Platyamphistoma* in the absence of a distinct median notch behind the acetabulum. The fact that the pharynx is smaller than the acetabulum in the new form distinguishes it readily from *Macropharynx* and the conical shape of the body and the presence of dorso-ventral bends in the caeca separate it from *Pseudoparamphistoma*. *Nilocotyle*, *Gigantoatrium*, *Glyptamphistoma*, *Platyamphistoma* and *Macropharynx* are known only from hippopotamus and *Pseudoparamphistoma* is found in carnivores: furthermore, with the exception of *Nilocotyle* and *Paramphistomoides*, these genera are characterized by a dorso-ventrally flattened body.

All the genera so far assigned to Orthocoelinae are characterized by the following: testes either directly or obliquely tandem, intercaecal and anterior to the acetabulum; ovary and Mehlis' gland posterior to the male gland; and the caeca always extending posteriorly beyond the testes. The present specimens differ from all these genera of Orthocoelinae in that the testes are symmetrically located laterally in the posterior third of the body, between the ends of the caeca and anterior border of the acetabulum, with the ovary and Mehlis' gland between them.

The presence of tegumental papillae on the wall of the genital atrium has been observed under light microscopy by previous workers who described them in the following amphistome species: *Paramphistomum papilligerum* Stiles & Goldberger, 1910; *Calicophoron papillosum* (Stiles & Goldberger, 1910); *Orthocoelium parvipapillatum* (Stiles & Goldberger, 1910); *Carmyerius wenyoni* (Leiper, 1908); *C. papillatus* Grétillat, 1962 and *C. parvipapillatus* Grétillat, 1962. The genital atrium of the new species also has papillae on the wall. The absence of a true ventral atrium (*sensu* Näsmark, 1937) distinguishes it from those of *P. papilligerum*, *C. wenyoni* and *C. papillatus*. Stiles & Goldberger (1910) gave no detailed description of the genital atria of *O. parvipapillatum* and *Calicophoron papillosum* but re-examination of the type material of the latter revealed the presence of a genital sphincter and sphincter papilla, features which are also found in *Bilatorchis papil-*

logenitalis. The type material of *O. parvipapillatum* could not be traced and it is very difficult to decide from the authors' illustrations if these features are present in this species. When suitably fixed materials of these and the new species become available, these tegumental papillae will be examined by transmission electron microscopy in an attempt to determine their nature and function.

Näsmark (1937) classified the genital atria of paramphistomids into different types based on the material available at that time but since no material of *Carmyerius wenyoni, Paramphistomum papilligerum, Calicophoron papillosum* and *Orthocoelium parvipapillatum* was available to him, their genital atria were not included in his scheme. Grétillat (1962), although aware that the genital atria of his species, *Carmyerius papillatus* and *C. parvipapillatus*, did not fit into any of those described by Näsmark (1937), made no attempt to designate a type name for this. Since the genital atrium described in this paper neither agrees with any of Näsmark's types nor was it given a type name by previous authors who had observed it, a type name "papillogenitalis" is now proposed, which is defined as follows: genital papilla moderately developed; genital and papillar sphincters present; genital atrium wall lined by tegumental papillae; true ventral atrium and ventral sphincter absent; radial musculature moderately developed. This type holds for *Calicophoron papillosum, Carmyerius parvipapillatus, Bilatorchis papillogenitalis* and, possibly, *Orthocoelium parvipapillatum*. The genital atria of *Paramphistomum papilligerum, Carmyerius wenyoni* and *C. papillatus* which are characterized by true ventral atria in addition to papillae may constitute another type.

From the same host and locality, Prudhoe, Yeh & Khalil (1964) have reported another amphistome, *Choerocotyloides onotragi*, which they attached to the subfamily Gastrodiscinae; this species is distinguished from the present specimens by the body being dorso-ventrally flattened, pharynx with pouches, caeca almost straight in their course, testes directly tandem and entirely intercaecal in location, different histological feature of the pharynx and the presence of a ciliated sperm canal dilatation (the ciliated chamber of Willmott & Pester, 1961).

As shown above, the species under consideration can readily be distinguished from all genera so far described in the sub-family Orthocoelinae on the basis of location and position of the genital organs and extent of the caeca. Such characters are considered of generic value for the superfamily Paramphistomoidea. For example, a similar character is used to separate two genera of the pouched amphistomes (Gastrothylacidae), *Carmyerius* Stiles & Goldberger, 1910 and *Fischoederius* Stiles & Goldberger, 1910. The testes are laterally symmetrical in the former but median and tandem in the latter. It seems justified, therefore, to erect a new genus and species for which *Bilatorchis papillogenitalis* is proposed.

Host: *Kobus leche* Gray, 1850

Habitat: rumen

Locality: Lochinvar, Zambia

Type specimens: holotype—Commonwealth Institute of Helminthology type collection number S1035/A
paratypes—Commonwealth Institute of Helminthology type collection number S1035/B; British Museum (Natural History) helminth collection number 1979.8.6.114–115; Swedish Museum of Natural History helminth collection numbers 3145–3146

Bilatorchis n.g.

Generic diagnosis

Orthocoelinae. Body oval to elongate, almost circular in cross section. Acetabulum subterminal, nilocotyle type. Pharynx paramphistomum type with few weakly developed middle circular muscle units. Oesophagus without muscular expansion, caeca with dorso-ventral bends extending posteriorly only to level of anterior borders of testes with blind ends directed ventrad. Testes laterally symmetrical in posterior third of the body, post caecal and antero-lateral to acetabulum. Pars prostatica and pars musculosa well developed and long. Ovary and Mehlis' gland intertesticular and intercaecal. Vitelline follicles in lateral fields extending from oesophageal

bifurcation to anterior border of testes. Genital atrium papillogenitalis type. Laurer's canal does not cross excretory vesicle or duct. Parasite of ruminants. Type and only species: *Bilatorchis papillogenitalis* n.g., n.sp.

Acknowledgements

The author wishes to thank Dr. L.F. Khalil under whose guidance this work was done, Dr. Sheila Willmott for her interest in this study, Dr. L.M. Gibbons for the kind assistance in many ways, particularly in scanning electron microscopy, and Dr. J.R. Lichtenfels for the loan of the type material of *Calicophoron papillosum.*

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Accepted for publication 21*st August*, 1979.

Additional remarks on Bilatorchis papillogenitalis Eduardo, 1980

Following what has been discussed elsewhere in this work concerning the paramphistomum (sensu Nasmärk, 1937) and calicophoron (sensu Dinnik, 1964) types of pharynx, that of the above species should now be referred to the latter type.

In the collection of Dr. J.A. Dinnik now housed in the Commonwealth Institute of Helminthology are sections of unidentified specimens from the rumen of Connochaetes taurinus (blue wildebeest) from Lochinvar Ranch, Monze, Zambia. These are identified here as Bilatorchis papillogenitalis and this constitutes a new host record for the species.

The genus Leiperocotyle Eduardo, 1980

INTRODUCTION

The writer (Eduardo, 1980c) erected the genus Leiperocotyle for Cotylophoron okapi Leiper, 1935 and C. congolense Baer, 1936 on the basis of the Laurer's canal wich does not cross the excretory vesicle or duct, the presence of a genital sucker and the well developed pars musculosa. The former species was designated as the type of the genus and was redescribed and illustrated based on the type specimens and additional materials. The published paper is here appended. Since Leiperocotyle congolense (Baer, 1936) was not redescribed nor illustrated in the paper, these are now provided here.

In the present study, Ceylonocotyle scoliocoelium var. benoiti Grétillat, 1966 was found to be a distinct species and belongs to the genus Leiperocotyle after re-examination of the type specimens loaned from the Musée Royal de l'Afrique Centrale, Tervuren. It is here redescribed and illustrated under a new name.

SYSTEMATIC PARASITOLOGY, 1 (3/4), 255–263 (1980).

A NEW GENUS, *LEIPEROCOTYLE*, FOR *COTYLOPHORON OKAPI* LEIPER, 1935 AND *C. CONGOLENSE* BAER, 1936 AND REDESCRIPTION OF *C. OKAPI*

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Summary

Leiperocotyle n.g. is erected for *Cotylophoron okapi* Leiper, 1935 and *C. congolense* Baer, 1936. The former is redescribed and illustrated from the type specimens and additional material from okapi in Zaïre (formerly Belgian Congo). The latter is regarded as a distinct and valid species and the features which distinguish it from *C. okapi* are discussed. The new genus is assigned to the subfamily Orthocoeliinae Price & McIntosh, 1953 but can be differentiated from all other genera in this subfamily by the well developed pars musculosa, the presence of a genital sucker and the less muscular genital papilla. The genus *Cochinocotyle* Gupta & Gupta, 1970 is synonymized with *Orthocoelium* (Stiles & Goldberger, 1910). The subgenus *Sellsitrema* Yamaguti, 1958 is raised to full generic rank and its diagnosis is given. A key to the genera of the subfamily Orthocoeliinae is provided.

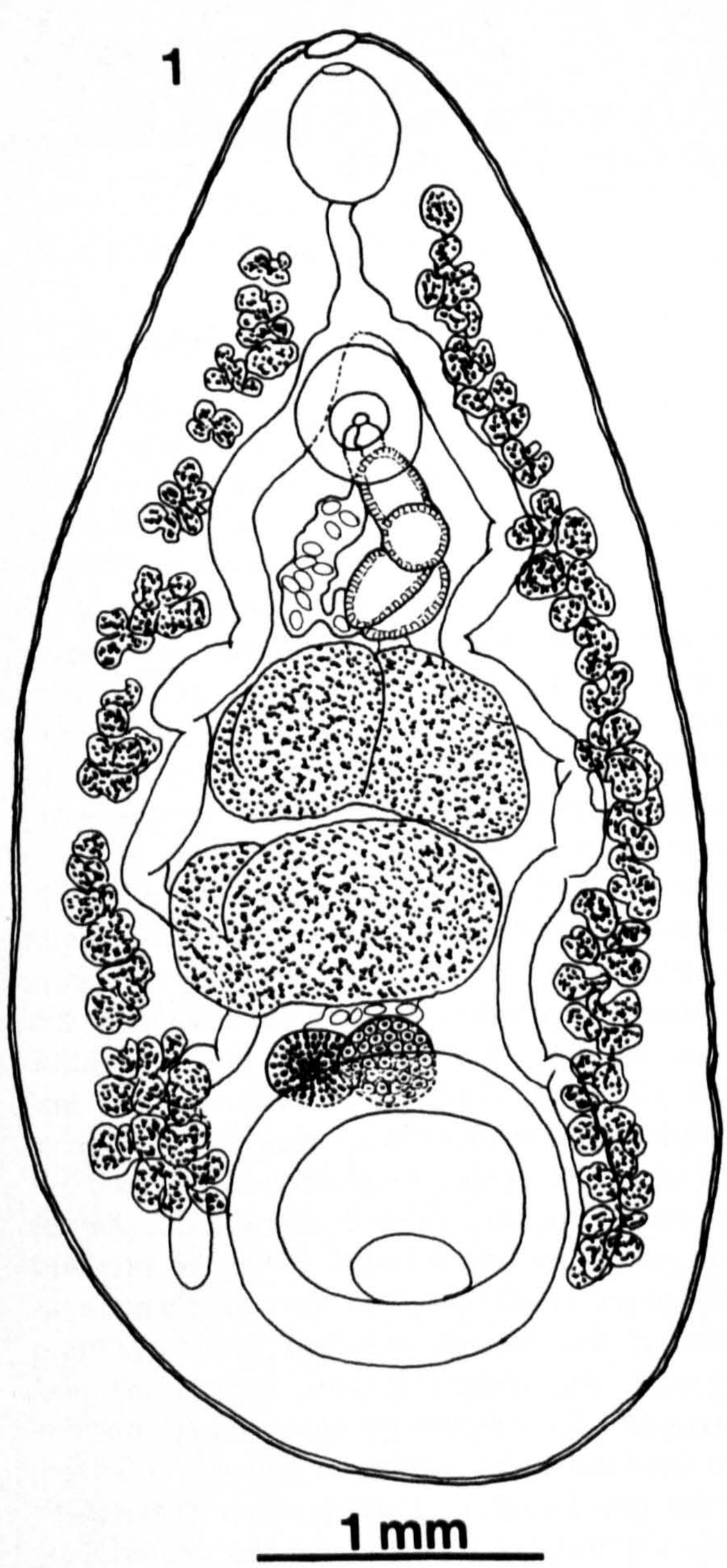
Introduction

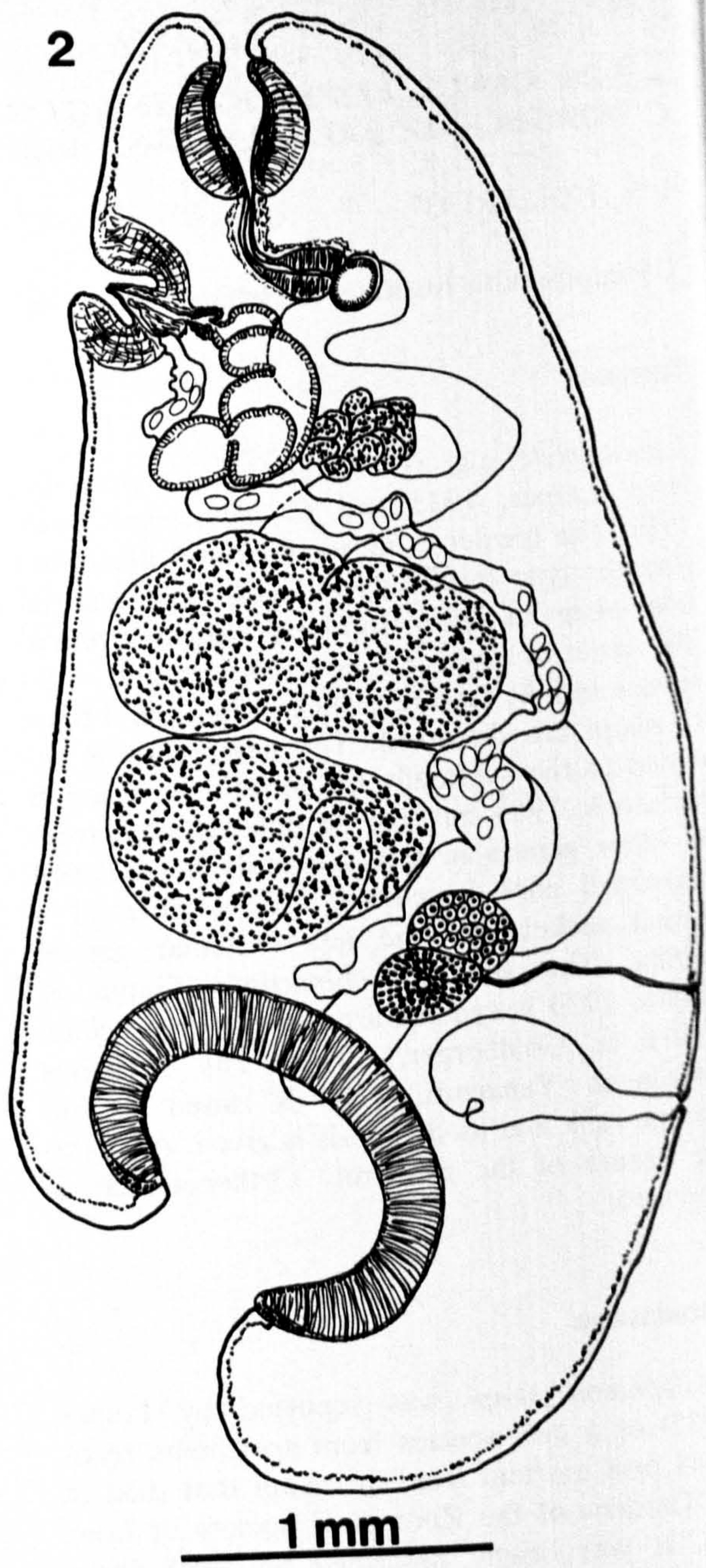
Cotylophoron okapi was reported by Leiper (1935) as a new species from specimens recovered post mortem from an okapi that died in the Gardens of the Zoological Society of London. It was briefly described as "with large testes, Laurer's canal and excretory duct do not cross" and was not illustrated. Baer (1936) described *C. congolense* from the same host but later (Baer, 1950) synonymized it with *C. okapi*. Price & McIntosh (1953) accepted Baer's synonymy but tentatively moved the species to the genus *Orthocoelium* (Stiles & Goldberger, 1910), as a new combination, because Laurer's canal does not cross the excretory vesicle or duct. This was accepted by Yamaguti (1971) since he included it in his list of species in the genus. The writer in a previous paper (Eduardo, 1980), having examined the type specimens of *C. okapi* pointed out that the species can be retained neither in the genus *Cotylophoron* nor in the genus *Orthocoelium*. In this study, the type specimens of *C. congolense* consisting of series of sections (loaned from the Muséum d'Histoire Naturelle, Genève) and few specimens in alcohol (loaned from the Musée Royal de l'Afrique Centrale, Tervuren) were also examined and these revealed that the species is not identical with *C. okapi*. This paper discusses the taxonomic position of both species with the proposal of a new genus, *Leiperocotyle*, for their reception. Characters which distinguish one species from the other are detailed. Since the previous description of *C. okapi* is very inadequate in terms of the present standard of amphistome diagnosis, the species is now redescribed and illustrated. The redescription is based on the type specimens and additional material collected by the late Dr. P. L. LeRoux from Zaïre (formerly the Belgian Congo). All this material is deposited in the helminth collection of the London School of Hygiene and Tropical Medicine now housed in the Commonwealth Institute of Helminthology. Representative specimens were also examined under the scanning electron microscope for surface topography.

Leiperocotyle okapi (Leiper, 1935) n.g., n. comb.

The body shape is oval to elongate depending on the state of contraction of the worm during

* Supported by a Scholarship Grant under the 4th Education Project of the Philippines with the World Bank.

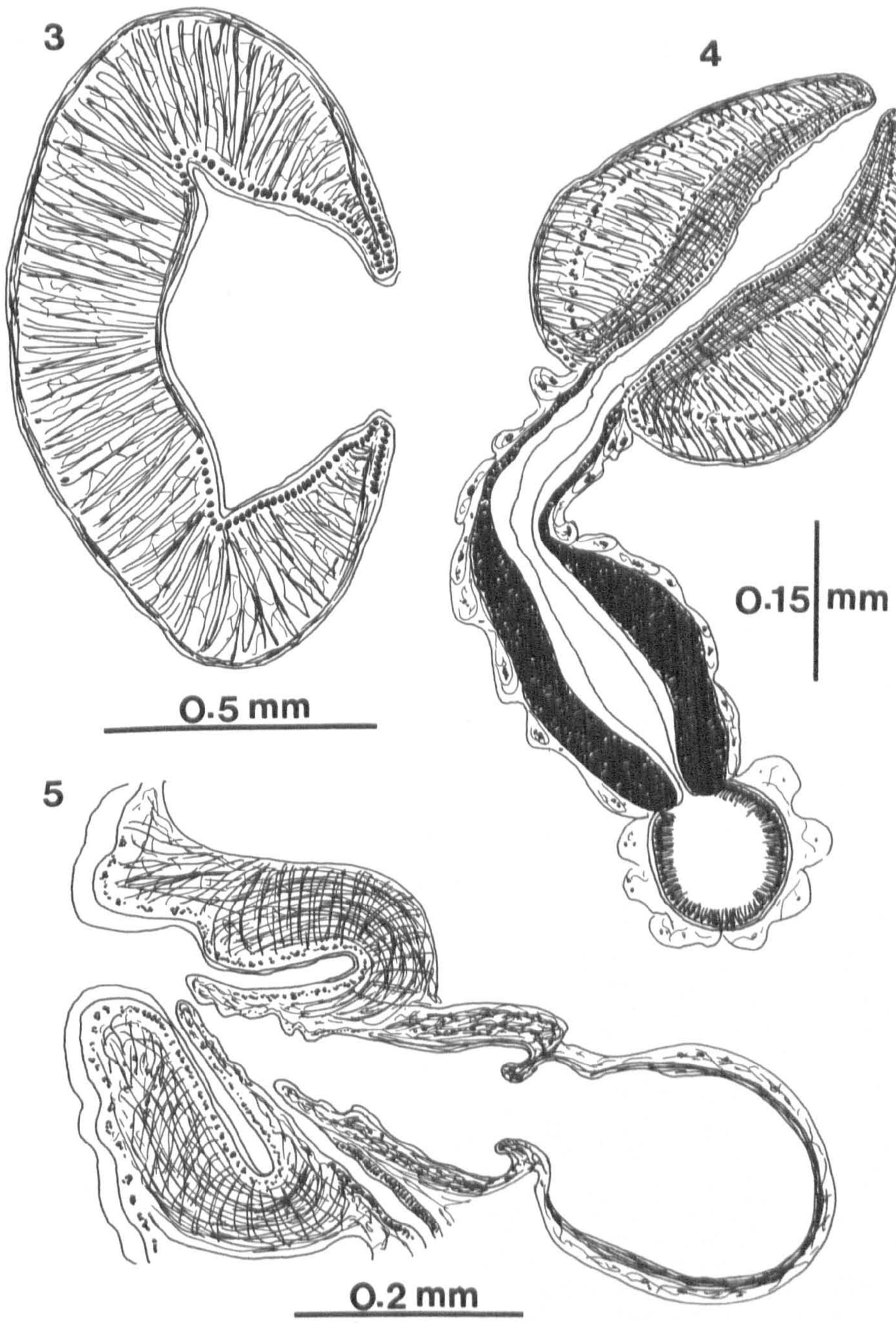




Leiperocotyle okapi
Fig. 1. Whole worm, ventral view;
Fig. 2. Whole worm, sagittal view.

fixation. Mature specimens are 2.90–5.01 mm long and are greatest in diameter (1.34–2.10 mm in the dorso-ventral direction and 2.00–2.62 mm from side to side) at the level of the testes or acetabulum.

The acetabulum is subterminal, with external diameter 1.00–1.24 mm in the dorso-ventral direction and its ratio to body length is 1:2.5 to 1:4.2. In median sagittal section (Fig. 3), it conforms to the cotylophoron type as defined by Näsmark (1937). The number of circular muscle units in each series is as follows: DE, 15–18; DI,



Leiperocotyle okapi
Fig. 3. Acetabulum, median sagittal section;
Fig. 4. Pharynx and oesophagus, median sagittal section;
Fig. 5. Genital atrium, median sagittal section.

30–43; VE, 11–16; VI, 31–42; dome, 8–10.

The pharynx is 0.37–0.53 mm long, 0.25–0.44 mm in the dorso-ventral direction and its ratio to body length is 1 : 7.2 to 1 : 10.4 and to the diameter of the acetabulum is 1 : 2.1 to 1 : 3. In median sagittal section (Fig. 4), it agrees with the paramphistomum type (*sensu* Näsmark, 1937) but a distinct middle circular muscle layer is present. The oesophagus is 0.44–0.66 mm long and the musculature of its wall expands in the posterior half to form an oesophageal bulb about 0.12–0.17 mm in diameter (Fig. 4). In well relaxed

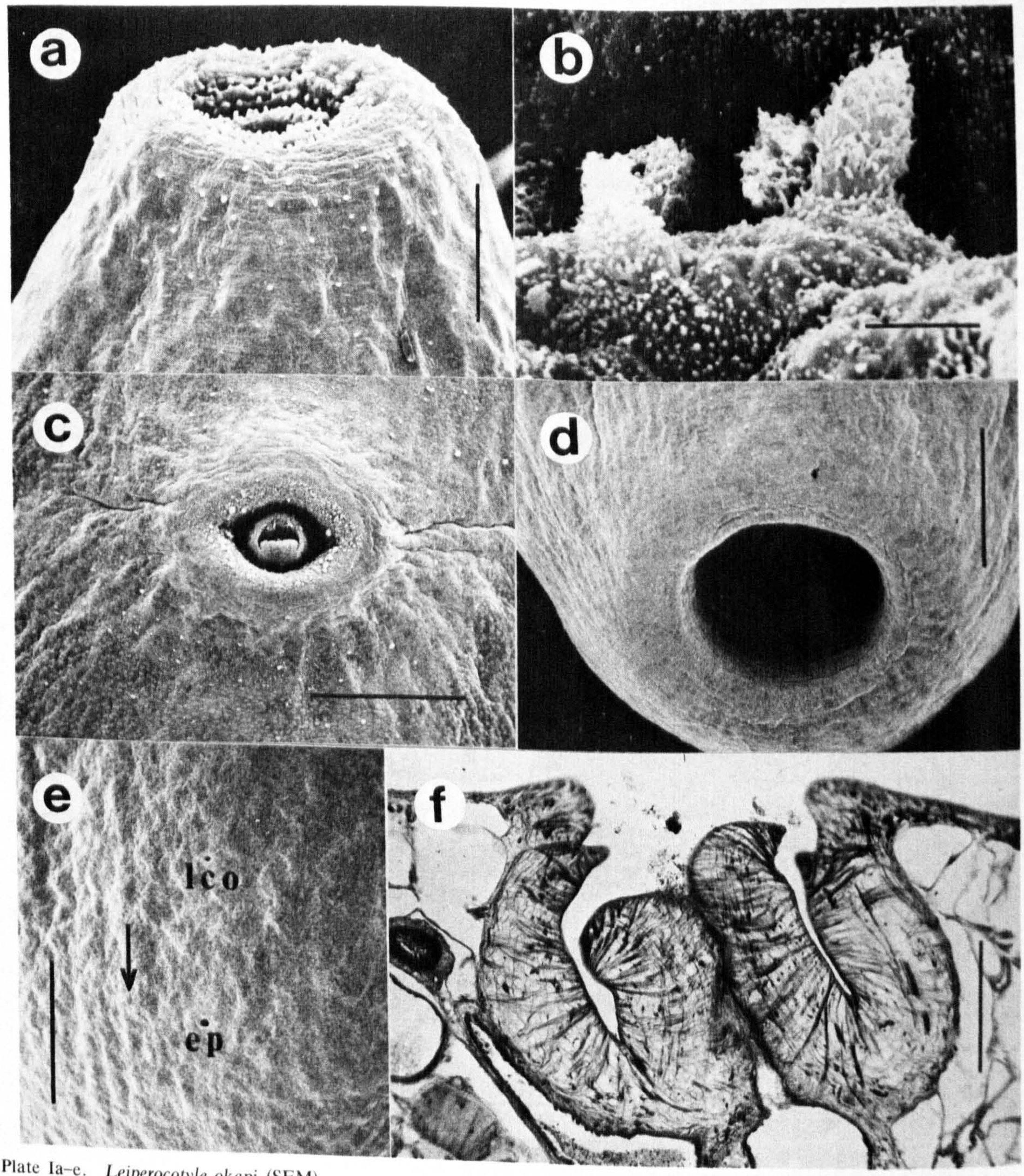


Plate Ia–e. *Leiperocotyle okapi* (SEM)

a. Anterior end showing tegumental papillae (scale bar, 150 μm);
b. Tegumental papillae on closer view, note hair-like processes covering surface (scale bar, 4 μm);
c. Genital opening, frontal view (scale bar, 300 μm);
d. Acetabular region, note absence of papilla (scale bar, 300 μm);
e. Postero-dorsal surface showing relation between the Laurer's canal opening (lco) and excretory pore (ep). Arrow indicates direction towards the posterior end (scale bar, 400 μm).

Plate If. *Sellsitrema sellsi.* Median sagittal section of the genital atrium of type specimen (LM). Note genital sucker and the very muscular genital papilla (scale bar, 170 μm).

specimens the oesophagus may appear almost straight but in contracted ones, it is bent dorsally from the point of origin of the caeca. The caeca run posteriorly down the lateral sides of the body making about four dorso-ventral bends. The blind ends terminate at the level of the acetabulum and are directed ventrally.

The lobed testes lie tandem in the posterior two thirds of the body between the acetabulum and the male ducts. The anterior testis measures 0.41–0.71 mm in length, 0.50–1.06 mm in width and 0.72–1.26 mm in the dorso-ventral direction and the posterior 0.41–0.68 mm in length 0.93–1.14 mm in width and 0.81–1.06 mm in the dorso-ventral direction. The pars prostatica is small and weakly developed. The coiled pars musculosa is well developed and about 0.21–0.22 mm in diameter. The thin-walled vesicula seminalis is also coiled and lies postero-dorsally to the pars musculosa.

The spherical ovary measures 0.21–0.30 by 0.21–0.35 mm and lies in the posterior third of the body anterodorsally to the acetabulum and postero-dorsally to the posterior testis. Mehlis' gland measures 0.17–0.29 by 0.25–0.48 mm and lies close to or slightly behind the ovary. Laurer's canal runs anteriorly to the excretory vesicle and opens on the dorsal surface about 0.102–1.90 mm anteriorly to the excretory pore (Figs. 2 & Plate Ie). The uterus runs dorsally to the testes and ventrally to the male ducts before it joins the metraterm to open into the genital pore on the ventral surface. Eggs are oval, operculate and, in utero, measure 91–122 by 50–67 μm. Large clusters of vitelline glands extend laterally from the level of the oesophagus to the level of the acetabulum.

The excretory vesicle lies dorsally to the acetabulum and its duct opens on the dorsal surface posteriorly to the opening of Laurer's canal.

The genital pore lies ventrally at the level of the oesophageal bifurcation or immediately posterior to it. The genital atrium is surrounded by a muscular sucker which, in median sagittal section (Fig. 5), is distinctly delimited from the surrounding parenchyma. The genital papilla is conical tapering towards its free end and has little musculature and no radial muscle fibres. This conforms to the cotylophoron type of genital atrium as described by Näsmark (1937). The genital sucker measures 0.31–0.36 mm in diameter and its ratio to the length of the pharynx is 1:1.1 to 1:1.4 and to the diameter of the acetabulum 1:2.5 to 1:3.6.

SEM examination of the body surface revealed tegumental papillae about 3.3–6.5 μm in height which appear to be covered by hair-like processes. These are present only on the anterior third of the body around the oral opening (Plate Ia–b).

Discussion

The generic position of *Cotylophoron okapi* and *C. congolense* has been uncertain. They were originally assigned to the genus *Cotylophoron* Stiles & Goldberger, 1910 by Leiper (1935) and Baer (1936), respectively. The latter author later (1950) considered the species to be synonymous and this was accepted by Yamaguti (1958). Price & McIntosh (1953) also accepted the synonymy but removed the species from the genus and tentatively assigned them to the genus *Orthocoelium* (Stiles & Goldberger, 1910). The move was accepted by Yamaguti (1971) but he gave no reason. However, Baer's original description of *C. congolense* and re-examination of the type specimens both show that this species is distinct from *C. okapi*. The characters in which they differ are as follows:

(i) the blind ends of the caeca in *C. congolense* are directed dorsally while those of *C. okapi* are directed ventrally;
(ii) the musculature of the posterior end of the oesophagus in *C. congolense* is provided with a small sphincter while that of *C. okapi* is developed into a muscular bulb;
(iii) the rim of the genital sucker in *C. congolense* has circular muscle bundles grouped to form a sphincter which is absent in *C. okapi*;
(iv) the vitellaria in *C. congolense* are confluent dorso-medially in their posterior limits while those of *C. okapi* are not.

The writer believes that these differences are

sufficient to establish both species as distinct and valid.

Although the genera to which these species have been allocated belong to the same family, they were assigned to different subfamilies—*Cotylophoron* to the Paramphistominae Fischoeder, 1901 *sensu stricto* (characterized by Laurer's canal crossing the excretory vesicle or duct) and *Orthocoelium* to the Orthocoeliinae Price & McIntosh, 1953 (in which Laurer's canal does not cross the excretory vesicle or duct). The present study has shown that both species belong to the Orthocoeliinae because Laurer's canal does not cross the excretory vesicle or duct, there are no pharyngeal pouches or diverticula and the body is not divided into two parts.

The Orthocoeliinae now contains the following genera: *Orthocoelium* (Stiles & Goldberger, 1910) (syn. *Ceylonocotyle* Näsmark, 1937); *Buxifrons* (Fukui, 1929) Näsmark, 1937; *Macropharynx* Näsmark, 1937; *Nilocotyle* Näsmark, 1937; *Gigantatrium* Yamaguti, 1958; *Glyptamphistoma* Yamaguti, 1958; *Paramphistomoides* Yamaguti, 1958; *Platyamphistoma* Yamaguti, 1958; *Pseudoparamphistoma* Yamaguti, 1958; *Cochinocotyle* Gupta & Gupta, 1970; and *Bilatorchis* Eduardo, 1980. The status of *Macropharynx* in the subfamily is questionable. The type and only species, *M. sudanensis* Näsmark, 1937 was described from one flattened specimen from the hippopotamus and it is not known if Laurer's canal crosses the excretory vesicle or duct and it has not been reported since. Yamaguti (1971) gave no reason for assigning it to the Orthocoeliinae.

Cochinocotyle, erected for a single species, *C. bovini* from cattle in India by Gupta & Gupta (1970) was based mainly on the histology of the acetabulum and the ratio of the diameter of the acetabulum to the length of the body: it was separated from *Ceylonocotyle* Näsmark, 1937, now a junior synonym of *Orthocoelium*. Attempts to obtain the type specimens for examination failed but the authors describe the acetabulum as being of the paramphistomum type, i.e. with the dorsal exterior circular muscle series divided into two groups. Their illustration of this structure in median sagittal section (Fig. 2) however differs from the description: what are labelled as DECM1 and DECM2 do not appear to be distinctly separated from each other by the oblique muscle fibres typical of the paramphistomum type. The acetabulum appears to consist of only one series of muscles with the units diminishing in size towards the interior end and, what is more, the number of dorsal exterior muscle bundles (DECM1 14 units and DECM2 12 units according to their description) is less than that of the ventral exterior series (28 to 29). This is not consistent with the paramphistomum type of acetabulum as, in all species known with this type, the number of circular units in the dorsal exterior series always exceeds that in the ventral exterior series. It seems more likely, therefore, that this acetabulum is of the streptocoelium type (*sensu* Näsmark, 1937) which is the type found in most species of *Orthocoelium*. *Cochinocotyle* was also differentiated from *Ceylonocotyle* on the basis of the ratio of the acetabulum to the length of the body. The values given were: 1:4.1 (whole mount) and 1:5.2 (median sagittal section) in the former and 1:6 to 1:7.2 in the latter. The difference in the ratio between the two genera is extremely small and as the authors had only two specimens of *Cochinocotyle* (one whole mount and the other sectioned for histological study) they could not allow for any variation caused by the state of the worm during fixation. Observations based on only two specimens are far from conclusive. *Cochinocotyle* Gupta & Gupta, 1970 therefore falls as a junior synonym of *Orthocoelium* (Stiles & Goldberger, 1910) and its only species becomes *O. bovini* (Gupta & Gupta, 1970) n. comb.

The genus *Nilocotyle* Näsmark, 1937 was divided by Yamaguti (1958) into two subgenera, namely, *Nilocotyle* (Näsmark, 1937) and *Sellsitrema* Yamaguti, 1958. These were separated from each other by the ratio of the acetabulum to the length of the body (acetabular index)—an unreliable character as indicated earlier. Under the subgenus *Sellsitrema* Yamaguti designated *Nilocotyle* (*Sellsitrema*) *sellsi* (Leiper, 1910) as the type and only species but failed to recognize one important character, namely, that the genital atrium is surrounded by a genital sucker. This readily separates it from all

other species in the genus. In Leiper's original description, the wall of the genital atrium is stated to be 0.15 mm thick and sharply delimited from the parenchyma and this is clearly illustrated. A re-examination of the type specimen of *Paramphistomum sellsi* revealed that the genital atrium is surrounded by a genital sucker (Plate If) which measures about 0.64 mm in diameter, has strong radial musculature and a wall which is clearly marked off from the surrounding tissue. The genital papilla is cylindrical, with the free end tending to expand outwards and muscular with strong radial fibres. Näsmark (1937) transferred the species to his genus, *Nilocotyle*, and designated its genital atrium "sellsi type" but he placed it with those forms lacking a genital sucker in his classification of the genital atria. Näsmark also described the cotylophoron type of genital atrium, as the only form with a genital sucker but as the sellsi type is also surrounded by a genital sucker it should be placed in the same group as the cotylophoron type. In the cotylophoron type, however, the genital papilla is less muscular, lacks radial musculature and tapers conically towards its free end thus differing from the sellsi type.

Since the type and only species of the subgenus *Sellsitrema* is readily distinguishable from *Nilocotyle* by characters which are considered to be of generic value, it is here proposed that it should be raised to full generic rank with characters as follows: Paramphistomidae, Orthocoeliinae; body conical; pars musculosa weakly developed; genital sucker present; genital papilla well developed and muscular. The diagnosis of *Nilocotyle* Näsmark, 1937 is therefore emended to include: genital sucker absent.

All the genera mentioned above can be differentiated from each other by a combination of morphological characters. For reasons given above, both *Cotylophoron okapi* and *C. congolense* belong to the subfamily Orthocoeliinae but they can neither be retained in the genus *Orthocoelium*, to which they were tentatively assigned, nor placed in any of the other genera in the subfamily. A new genus, *Leiperocotyle*, is therefore erected for their reception, named after the late Prof. R. T. Leiper who first reported an amphistome from the okapi.

The well developed pars musculosa in both these species resembles that of *Orthocoelium* and *Bilatorchis* but they differ from both in the presence of a genital sucker and in having a different type of acetabulum and from the latter in the tandem and intercaecal position of the testes and the post-testicular location of the ovary and Mehlis' gland. They closely resemble *Sellsitrema* and *Platyamphistoma* in possessing a genital sucker but differ from both in having a well developed pars musculosa, a different type of acetabulum and from the latter in not being flattened dorso-ventrally and in lacking a notch behind the acetabulum. Although all three genera have genital atria with a genital sucker, that of *Sellsitrema* and *Platyamphistoma* is of the sellsi type and that of *Leiperocotyle* is of the cotylophoron type. *Sellsitrema* and *Platyamphistoma* are so far known only from hippopotamus. *Leiperocotyle* differs from the remaining genera in the subfamily, namely, *Buxifrons*, *Nilocotyle*, *Gigantatrium*, *Glyptamphistoma*, *Pseudoparamphistoma* and *Paramphistomoides* in possessing a well developed pars musculosa and a genital sucker and in having a different type of acetabulum. In addition, *Buxifrons* is concave ventrally like a leaf, *Gigantatrium* possesses an enormous genital atrium, *Glyptamphistoma* has transverse parallel hoof-like thickenings on the body surface and *Pseudoparamphistoma* is thin, translucent and flattened dorso-ventrally.

Leiperocotyle n.g.

Diagnosis:

Paramphistomidae, Orthocoeliinae. Body oval to elongate, almost circular in cross section, Acetabulum subterminal. Pharynx without diverticula. Testes lobed, tandem, pre-ovarian and intercaecal. Pars musculosa well developed; pars prostatica small and weakly developed. Ovary and Mehlis' gland post-testicular. Genital sucker present; genital papilla less muscular. Laurer's canal does not cross excretory vesicle or duct. Parasites of ruminants.

Type species: *Leiperocotyle okapi* (Leiper, 1935) n. comb.

Other species; *Leiperocotyle congolense* (Baer, 1936) n. comb. Two other species are tentatively assigned to the

new genus pending re-examination of the type specimens: *Leiperocotyle orientalis* (Harshey, 1934) n. comb. (=*Cotylophoron orientalis* Harshey, 1934) and *Leiperocotyle elongatum* (Harshey, 1934) n. comb. (=*Cotylophoron elongatum* Harshey, 1934), both from sheep and goat in India.

To accommodate the new genus under Orthocoeliinae, the subfamily diagnosis is emended to include: genital sucker present or absent, genital papilla well or weakly developed and muscular or not.

Although most mammalian paramphistomids parasitize a wide range of hosts belonging to the same suborder or family, *Leiperocotyle okapi* and *L. congolense* appear to be restricted only to the okapi. The only record of the presence of the former in other hosts, *Adenota varondi* and *Tragelaphus scriptus*, by Manter and Pritchard (1964) is a case of misidentification. The writer has re-examined their original material (loaned from the Musée Royal de l'Afrique Centrale, Tervuren) and this revealed that Laurer's canal crosses the excretory vesicle or duct and that the specimens are identical with the type specimens of *Cotylophoron fuelleborni* Näsmark, 1937 (loaned from the Zoologisches Museum der Humboldt Universität zu Berlin).

Key to the Genera of the subfamily Orthocoeliinae

1.	Pars musculosa well developed	2
	Pars musculosa weakly developed	4
2.	Genital sucker present, genital papilla with little musculature	*Leiperocotyle n.g.*
	Genital sucker absent ..	3
3.	Testes tandem or oblique and intercaecal, ovary and Mehlis' gland post-testicular	*Orthocoelium* (syn. *Ceylonocotyle, Cochinocotyle*)
	Testes horizontal, one on each lateral side and postcaecal; ovary and Mehlis' gland intertesticular	*Bilatorchis*
4.	Genital sucker present, genital papilla very muscular	*Sellsitrema*
	Genital sucker absent ..	5
5.	Genital atrium enormous	*Gigantatrium*
	Genital atrium not enormous	6
6.	Body concave ventrally like a leaf	*Buxifrons*
	Body with tranverse parallel hoof-like thickenings	*Glyptamphistoma*
	Body thin, transluscent and flattened dorsoventrally	*Pseudoparamphistoma*
	Body neither concave ventrally nor with hoof-like thickenings nor flattened dorsoventrally	7
7.	Vitellaria extensive, parasite of ruminants ..	*Paramphistomoides*
	Vitellaria not extensive, parasite of hippopotamus	*Nilocotyle*

The genus *Macropharynx* is omitted because it is not known whether Laurer's canal crosses the excretory vesicle or duct or not. Nevertheless, the enormous pharynx, which is larger than the acetabulum, separates it readily from all the above genera.

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alcohol and Manter & Pritchard's original material of *C. okapi*), Dr. Claude Vaucher (type specimens of *C. fuelleborni*). The technical assistance of Mrs. May Getley is gratefully acknowledged.

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Leiperocotyle congolense (Baer, 1936) Eduardo, 1980

TYPE SPECIMENS: Muséum d'Histoire Naturelle, Genève
(Coll. No. c/53-78, microscopic sections)
Musée Royal de l'Afrique Centrale, Tervuren
(specimens in alcohol)

OTHER MATERIAL EXAMINED: Host, locality and donor/collection

Okapia johnstoni	Angunu, Zaire	British Museum (Natural History) coll. no. 1973.9.16.6-106, in the Chandone-Peel collection.

HABITAT: Stomach

DESCRIPTION:

Body conical, nearly straight, 6.00-8.52 mm lcng, 2.01-3.52 mm in greatest width in the dorso-ventral direction.

Acetabulum subterminal, 1.00-2.64 mm in external diameter in the dorso-ventral direction; ratio to body length 1:3.2 to 1:5; of the cotylophoron type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units,d.e.c., 14-18; d.i.c., 40-51; v.e.c., 10-15; v.i.c., 48-61; m.e.c., 12-18.

Pharynx 0.80-0.92 mm long, 0.74-0.92 mm wide in the dorso-ventral direction; ratio body length 1:7.8 to 1:9.5, to the diameter of the acetabulum 1:2 to 1:3; of the calicophoron type (sensu Dinnik, 1964) with distinct middle circular series. Oesophagus 0.65-0.76 mm long, musculature of wall relatively thin but thickened in its posterior end to form a small sphincter, lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form dorso-ventral bends during the course, reach level of acetabulum with the blind ends directed dorsally.

Testes lobed, tandem in posterior part of the body; anterior testis 0.63-0.86 mm long, 0.92-1.13 mm in the dorso-ventral direction; posterior testis 0.82-1.03 mm long, 1.02-1.33 mm in the dorso-ventral direction. Seminal vesicle thin-walled and deeply coiled; pars musculosa thick-walled, well developed and convoluted; pars prostatica very weakly developed and sometimes indistinct.

Ovary subspherical, 0.42-0.48 by 0.49-0.50 mm, posterior to testes and anterior to acetabulum; Mehlis' gland close to ovary, 0.32-0.37 by 0.35-0.39 mm; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface about 0.29-0.36 mm anteriorly to the excretory pore; uterus winds forward, dorsal to the testes them ventral to the male ducts; vitellaria in lateral fields, extend from level of pharynx to acetabulum, confluent dorso-medially in their posterior limit; egg 130-144 by 58-61 µm.

Genital pore opens on the ventral surface at a level posterior to the oesophageal bifurcation; terminal genitalium of the schistocotyle type (sensu Sey and Graber, 1979a), genital sucker about 0.86-0.94 mm in diameter.

Excretory vesicle antero-dorsal to acetabulum; excretory vesicle opens on the dorsal surface posteriorly to the Laurer's canal opening.

FIGURE 159

Leiperocotyle congolense (Baer, 1936) Eduardo, 1980

a. Whole worm, sagittal view

b. Cross section at region of the pharynx

c. Cross section at region of the acetabulum

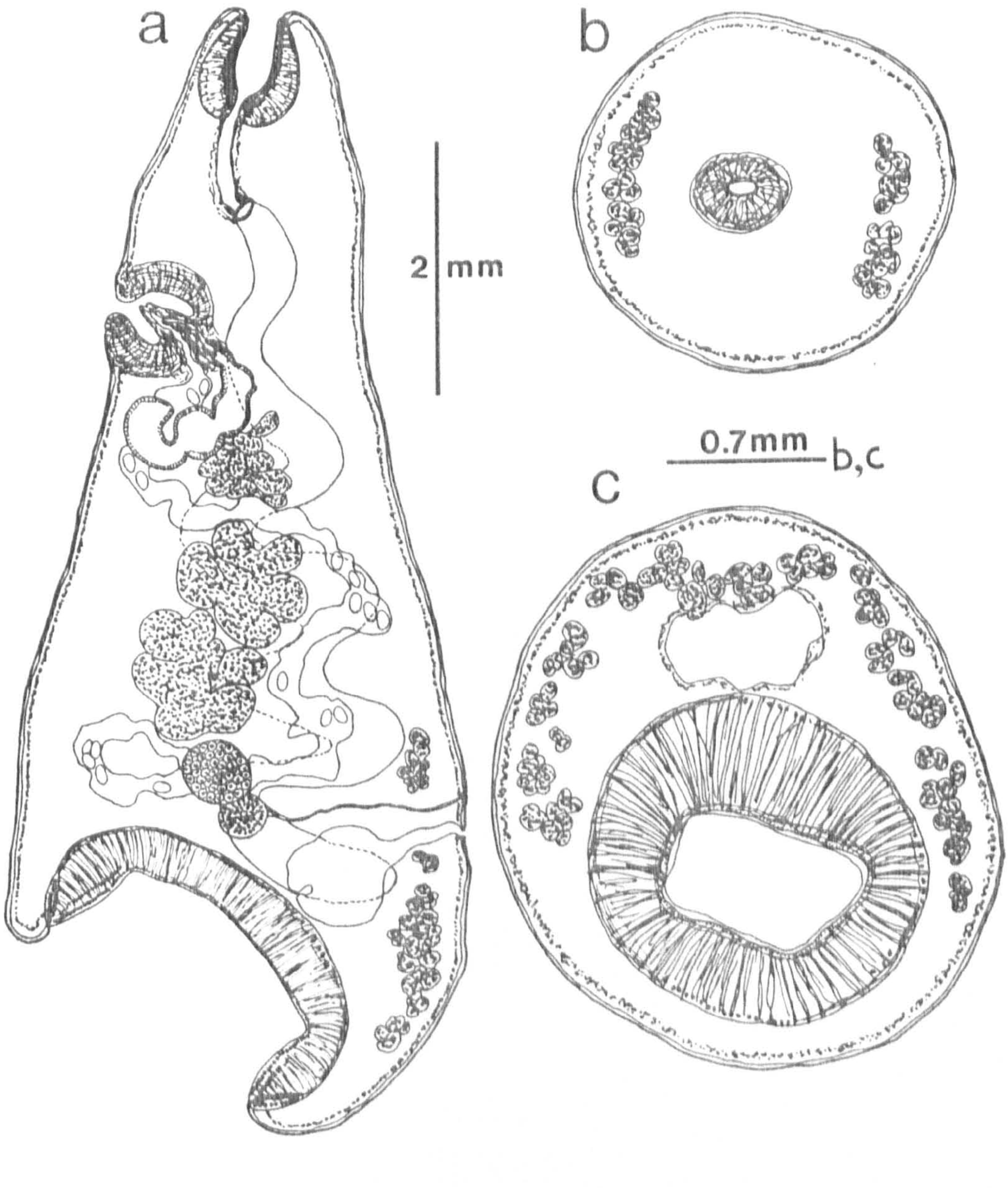

a
2 mm
b
0.7mm b,c
c

FIGURE 160

Leiperocotyle congolense (Baer, 1936) Eduardo, 1980

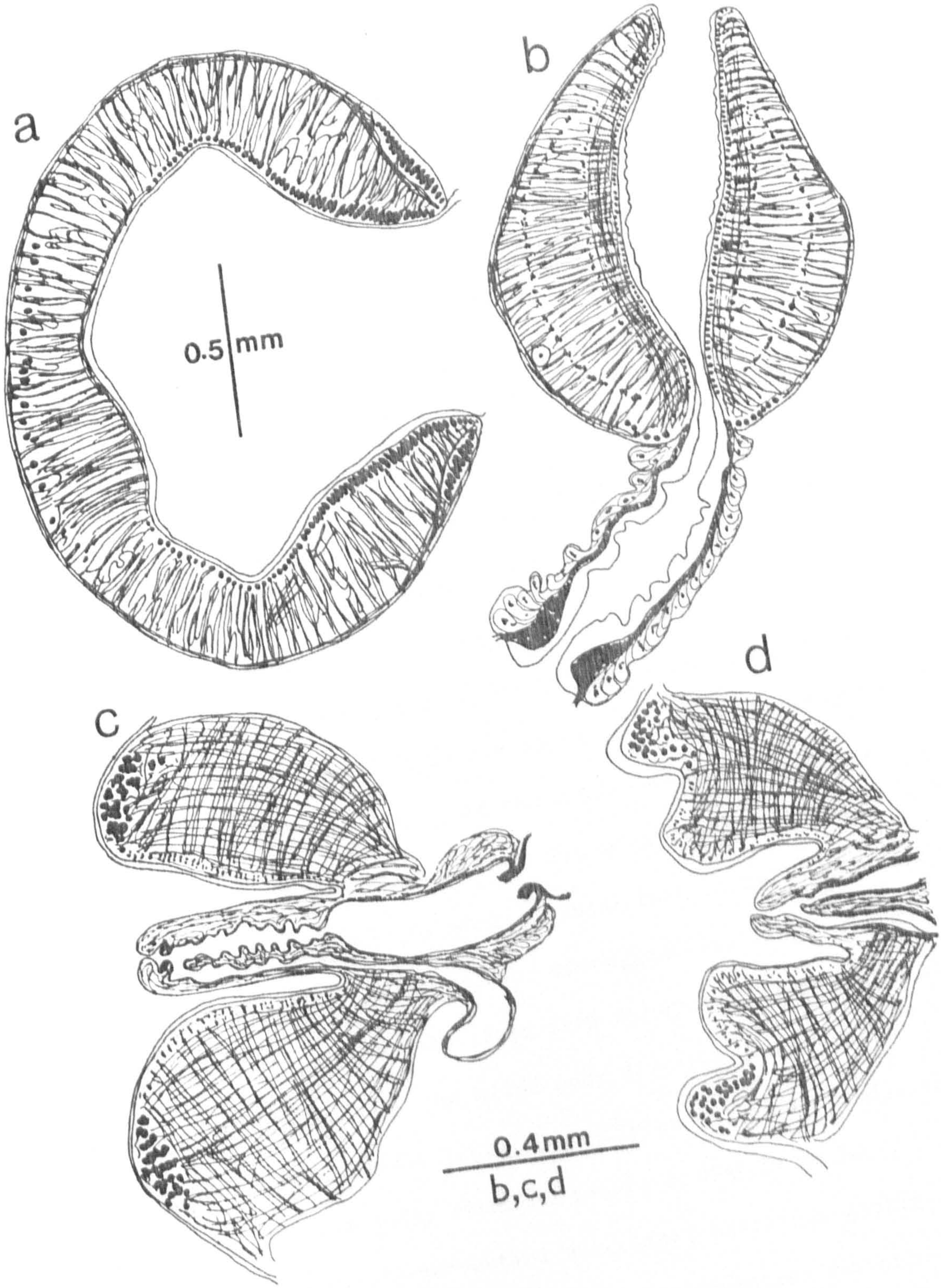
(median sagittal section)

a. Acetabulum (cotylophoron type)

b. Pharynx (calicophoron type) and oesophagus, note posterior sphincter of oesophagus

c. Terminal genitalium (schistocotyle type), relaxed form

d. Terminal genitalium (schistocotyle type), partly retracted form


a
0.5 mm
b
d
C
0.4mm
b,c,d

Leiperocotyle gretillati nomen novum

(For Ceylonocotyle scoliocoelium var. benoiti Grétillat, 1966)

TYPE SPECIMENS: Musée Royal de l'Afrique Centrale, Tervuren (Coll. No. 30352-30451) from the intestines of a "black buffalo" in the Belgian Congo (now Zaire).

DESCRIPTION:

Body small, conical, 2.38-2.90 mm long, 1.40-1.51 mm in greatest width in the dorso-ventral direction. Body surface has papillae on the anterior end around the oral opening.

Acetabulum subterminal, 0.75-0.96 mm in external diameter in the dorso-ventral direction; ratio to body length 1:3.3 to 1:3.8; of the cotylophoron type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 10-16; d.i.c., 30-41; v.e.c., 11-14; v.i.c., 35-46; m.e.c., 7-18.

Pharynx 0.57-0.65 mm long, 0.38-0.62 mm in the dorso-ventral direction; ratio to body length 1:4 to 1:5.2, to the diameter of the acetabulum 1:1.1 to 1:1.4; of the calicopharon type (sensu Dinnik, 1964) in median sagittal section with distinct middle circular series. Oesophagus short, musculature of wall relatively thin, lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form deep dorso-ventral bends, reach level of acetabulum with the blind ends directed dorsally.

Testes small, deeply lobed, directly or obliquely tandem in middle third of the body; anterior testis 0.20-0.25 mm long, 0.24-0.27 mm in the dorso-ventral direction; posterior testis 0.20-0.23 mm long, 0.27-0.30 mm in the dorso-ventral direction.

Seminal vesicle thin-walled and deeply coiled; pars musculosa thick-walled, relatively well developed and convoluted; pars prostatica very weakly developed.

Ovary small, 0.09-0.13 by 0.09-0.14 mm, posterior to testes and anterior to acetabulum; Mehlis' gland close to ovary, 0.60-0.09 by 0.06-0.07 mm; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface about 0.07-0.16 mm anteriorly to the excretory pore; uterus winds forward, dorsal to the testes then ventral to the male ducts; vitellaria in lateral fields, consist of few groups of small follicle, extend from level of the oesophageal bifurcation to ovary just anterior to the acetabulum, not confluent dorso-medially in their anterior and posterior limits; egg not seen as all specimens examined were young.

Genital pore opens on the ventral surface at level of the oesophageal bifurcation or just posterior to it; terminal genitalium of the cotylophoron type (sensu Näsmark, 1937); genital sucker 0.27-0.47 mm in diameter.

Excretory vesicle antero-dorsal to acetabulum; excretory pore opens on the dorsal surface posteriorly to the Laurer's canal opening.

FIGURE 161

Leiperocotyle gretillati nomen novum

a. Whole worm, ventral view

b. Whole worm, sagittal view

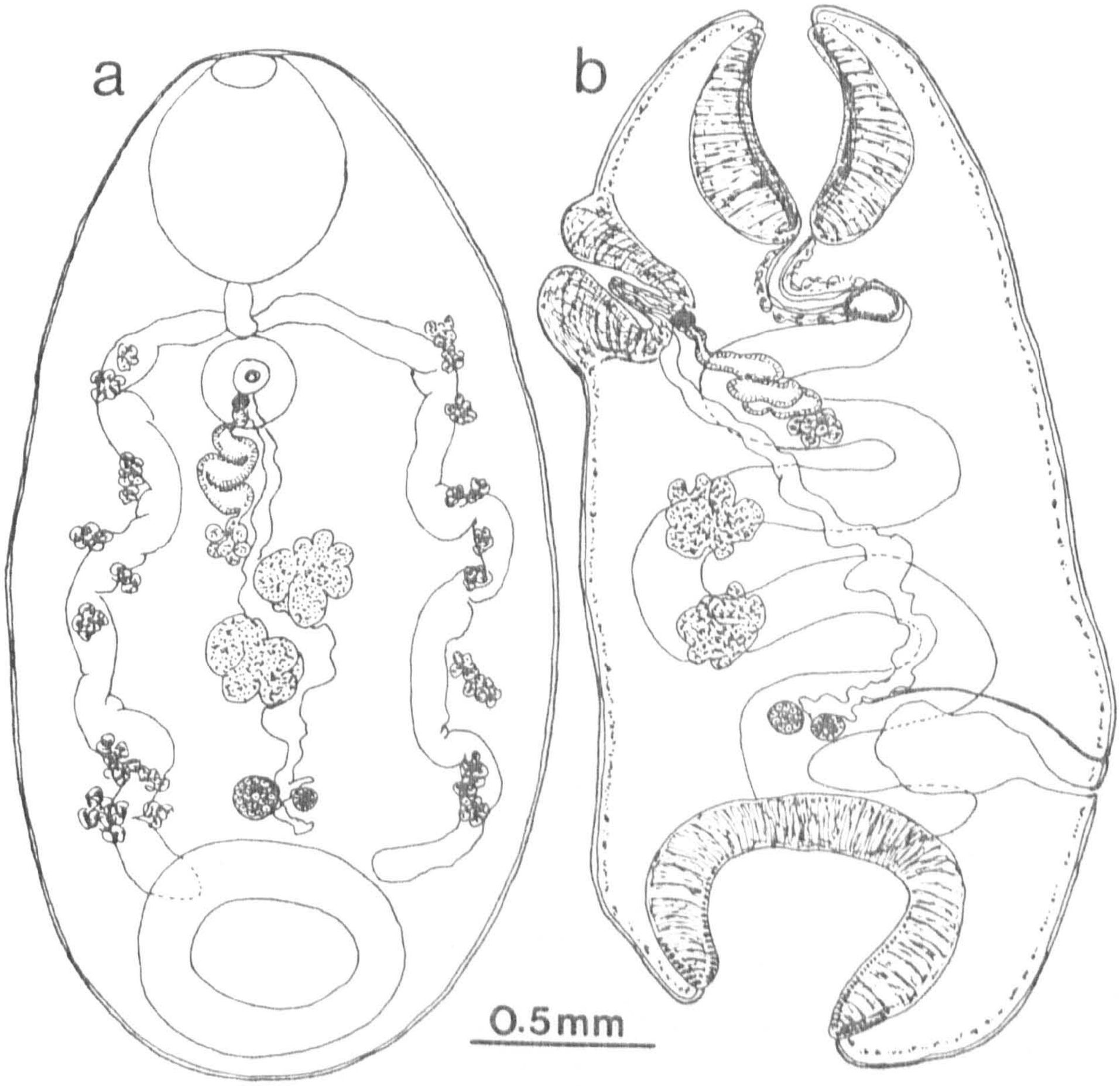

a
b
0.5mm

FIGURE 162

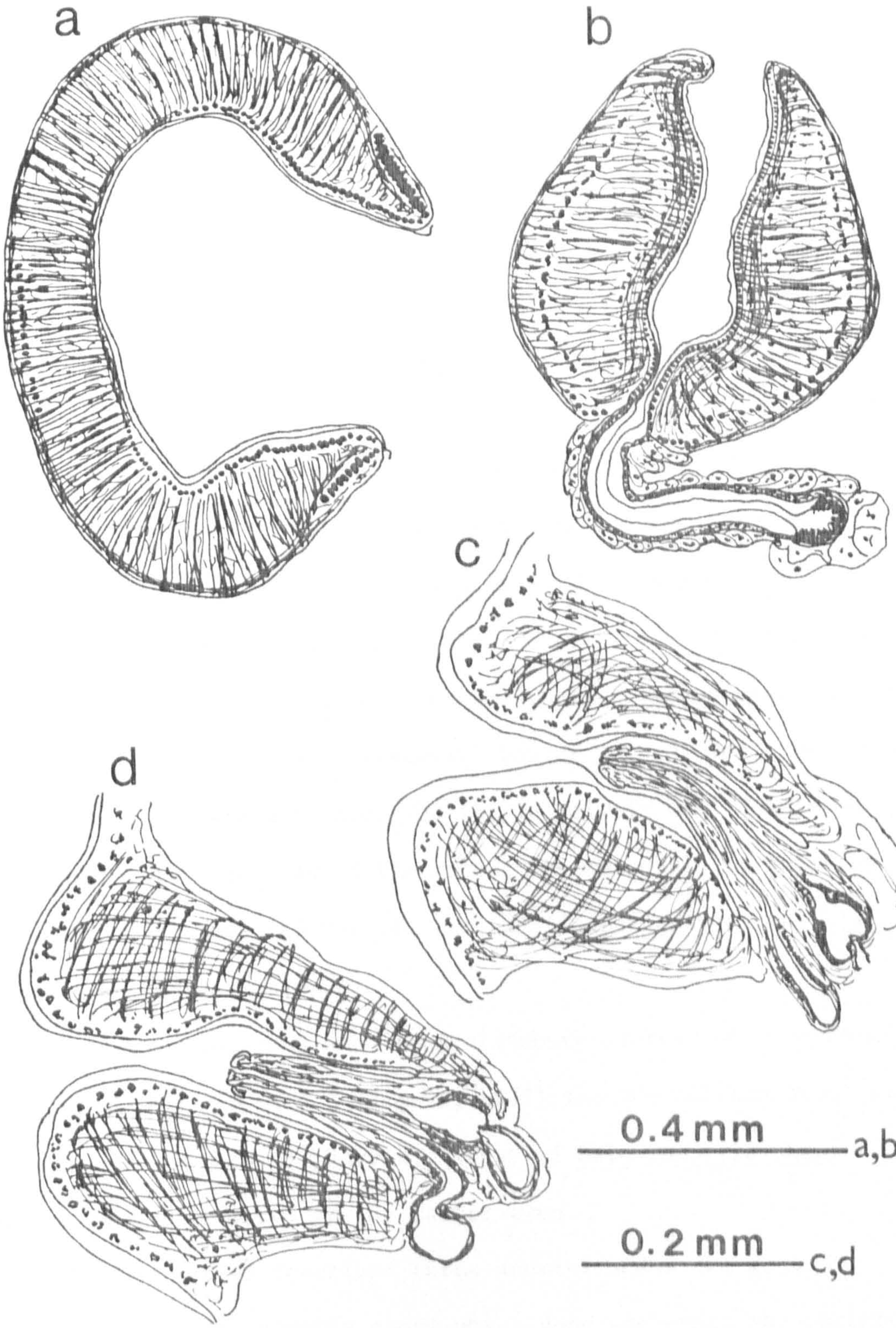
Leiperocotyle gretillati nomen novum

(median sagittal section)

a. Acetabulum (cotylophoron type)

b. Pharynx (calicophoron type) and oesophagus

c - d. Terminal genitalium (cotylophoron type)


a
b
C
d
0.4 mm
a,b
0.2 mm
c,d

DISCUSSION

The type specimens of the forms described by Grétillat (1966) as Ceylonocotyle scoliocoelium var. benoiti as new variety from the intestine of a black buffalo in Zaire was re-examined in this study, loaned from the Musée Royal de l'Afrique Centrale, Tervuren. It was observed that the species is not at all related to Ceylonocotyle scoliocoelium nor it belongs to the genus Ceylonocotyle (now Orthocoelium). What was regarded as a well developed genital sphincter is in fact a genital sucker and this clearly shown in Grétillat's illustrations (Figs. 6 & 7) of the species. A weakly developed pars prostatica was also observed, instead of a long one as was originally described. Grétillat has mistaken part of a large lymphatic trunk as the pars prostatica. In young specimens such as his, lymphatic and excretory vessels are very prominent. The species in question belongs to the genus Leiperocotyle because of the presence of a genital sucker, Laurer's canal does not cross the excretory vesicle or duct and the relatively well developed pars musculosa. In view of the above, the material in question requires a new name and for it, the name Leiperocotyle gretillati nomen novum is here proposed.

Following what has been said elsewhere in this work concerning the paramphistomum (sensu Näsmark, 1937) and the calicophoron (sensu Dinnik, 1964) types of pharynx, that of Leiperocotyle okapi should now be referred to the latter type.

Harshey (1934) described three species under the genus Cotylophoron with Laurer's canal which does not cross the excretory vesicle or duct namely, Cotylophoron ovatum, C. orientalis and

C. elongatum, all from sheep and goats in India. Because of the above character, Price and McIntosh (1953) tentatively moved them to the genus Orthocoelium. Mukherjee and Chauhan (1965) regarded C. ovatum as a synonym of Ceylonocotyle (now Orthocoelium) scoliocoelium and C. orientalis and C. elongatum as synonyms of Cotylophoron indicum Stiles and Goldberger, 1910, a species which is regarded here a synonym of Paramphistomum epiclitum. Bhattacharyulu and Pande (1969) considered C. ovatum as species inquirenda. Although three species were described by Harshey (1934) to possess a genital sucker, his illustration of the cross section of C. ovatum (Fig. 2) through the genital pore region clearly indicates the absence of this structure. Its absence and other features given in the original description conform with Orthocoelium scolicoelium. The writer agrees with Mukherjee and Chauhan (1965) for the proposed synonymy of C. ovatum with O. scoliocoellium. Cotylophoron orientalis and C. elongatum were not illustrated by Harshey in cross sections, thus the alledged presence of a genital sucker in both species could not be verified. Eduardo (1980c) moved tentatively both species to the genus Leiperocotyle pending re-examination of the type specimens. However, despite several efforts, the type specimens could not be traced and no new materials could be obtained. Although from the original description, both species have features in common with the genus Leiperocotyle, i.e. presence of a genital sucker, Laurer's canal does not cross the excretory vesicle or duct and a well developed pars musculosa, their specific status could not be accurately determined because of the lack of information on histological details and other morpho-

logical features. In view of the above, the writer regards Cotylophoron orientalis Harshey, 1934 and C. elongatum Harshey, 1934 as species inquirendae.

The three species assigned to the genus Leiperocotyle are separable by a key given below.

Key to the species of the genus Leiperocotyle Eduardo, 1980

1. Oesophageal bulb present; caecal ends directed ventrally - L. okapi

   Oesophageal bulb absent; caecal ends directed dorsally - 2

2. Vitellaria confluent dorso-medially in their posterior limit; posterior oesophageal sphincter present; terminal genitalium of the schistocotyle type - - - - L. congolense

   Vitellaria not confluent dorso-medially; posterior oesophageal sphincter absent; terminal genitalium of the cotylophoron type - - - - - - - - - - - L. gretillati

The genus Stephanopharynx Fischoeder, 1901

INTRODUCTION

The genus Stephanopharynx was erected by Fischoeder (1901, 1902, 1903) for a new species which he described as Stephanopharynx compactus from Bos taurus in Africa. Since then, only two species have been added to the genus namely, Stephanopharynx secundus Stunkard, 1929 from Redunca bohor (=Redunca redunca) and S. coilos Dollfus, 1963 from Hippotragus equinus, both from Africa. As will be shown in the discussion, the latter two species are junior synonyms of the former. Stephanopharynx compactus is redescribed and illustrated here based on specimens from various ruminants in Africa

GENERIC DIAGNOSIS

Paramphistomidae, Stephanopharynginae. Body conical with rounded ends. Acetabulum subterminal or nearly terminal. Pharynx with enormous and unpaired pouch or diverticulum; caeca form deep and irregular dorso-ventral bends. Testes lobed, tandem; pars musculosa well developed; cirrus pouch absent. Ovary and Mehlis' gland posttesticular; Laurer's canal does not cross the excretory vesicle or duct; vitellaria in lateral fields. Genital sucker absent. Parasitic in the stomach of ruminants.

Type species: Stephanopharynx compactus Fischoeder, 1901

Stephanopharynx compactus Fischoeder, 1901

Synonyms: Stephanopharynx secundus Stunkard, 1929
Stephanopharynx coilos Dollfus, 1963

TYPE SPECIMENS: Not available for examination

MATERIALS EXAMINED: Hosts, localities and donors/collection

Cattle	Mbesuma, Chinsali Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Connochaetes taurinus	Lochinvar Ranch, Monze, Zambia	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.
Hippotragus equinus	Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Kobus kob	Katagum, Nigeria	London School of Hygiene & Tropical Medicine
Kobus leche	Zambia	London School of Hygiene & Tropical Medicine, Dr. P.L. LeRoux collection.
Redunca arundinum	Quimbango, Malanga, Angola	Commonwealth Institute of Helminthology, Dr. J.A. Dinnik collection.

HABITAT: Rumen

DESCRIPTION:

Body conical with rounded ends, 2.99-9.58 mm long, 1.88-4.83 mm in greatest width in the dorso-ventral direction. Body surface has dome-shaped papillae around the oral opening and on the area around the genital pore. Those on the latter are much larger and more densely arranged than those on the former.

Acetabulum subterminal or nearly terminal, 1.01-2.32 mm in external diameter in the dorso-ventral direction; ratio to body length 1:2.1 to 1:4.6; of the stephanopharynx type (sensu Näsmark, 1937) in median sagittal section; number of circular muscle units, d.e.c., 33-46; d.i.c., 48-59; v.e.c., 35-48; v.i.c., 40-48; m.e.c., 4-10.

Pharynx 0.43-1.16 mm long, 0.69-1.62 mm in the dorso-ventral direction; ratio to body length 1:5.9 to 1:10, to the diameter of the acetabulum 1:1.6 to 1:2.8. It has an enormous unpaired pouch or diverticulum measuring about 1.10-3.91 mm long, on the internal surface of the diverticulum are long slender papillae of varying length, concentrated and present only on the lateral corners. In median sagittal section, the pharynx is of the stephanopharynx type (sensu Näsmark, 1937). Oesophagus 1.20-1.36 mm long, usually bend dorsally; musculature of wall relatively thick, without bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form very deep and irregular dorso-ventral bends, reach level of acetabulum with the blind ends directed posteriorly.

Testes lobed, tandem in posterior two third of the body; anterior testis 0.33-0.87 mm long, 0.74-2.03 mm in the dorso-ventral direction; posterior testis 0.34-0.87 mm long, 0.87-1.88 mm in the dorso-ventral direction. Seminal vesicle thin-walled, relatively short and coiled; pars musculosa thick-walled, relatively well developed; pars prostatica 0.32-0.35 by 0.12-0.26 mm.

Ovary subspherical, 0.14-0.51 by 0.29-0.63 mm, posterior to testes and anterior to acetabulum; Mehlis' gland close to ovary,

0.17-0.25 by 0.25-0.87 mm; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface about 0.63-0.66 mm anteriorly to the excretory pore; uterus winds forward, dorsal to the testes then ventral to the male ducts; vitellaria in lateral fields, extend from level of the oesophageal bifurcation to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 130-138 by 67-75 µm.

Genital pore opens on the ventral surface at a level posterior to the oesophageal bifurcation; terminal genitalium of the stephanopharynx type (sensu Näsmark, 1937) in median sagittal section.

Excretory vesicle antero-dorsal to acetabulum; excretory pore opens on the dorsal surface posteriorly to the Laurer's canal opening.

FIGURE 163

Stephanopharynx compactus Fischoeder, 1901

(SEM)

a. Oral end, not small papillae (scale bar = 100 µm)

b. Genital pore region, note large papillae
(scale bar = 200 µm)

c. Closer view of papillae around genital pore
region, note dome shape and smooth surface
(scale bar = 100 µm)

d. Closer view of genital papilla (scale bar = 200 µm)

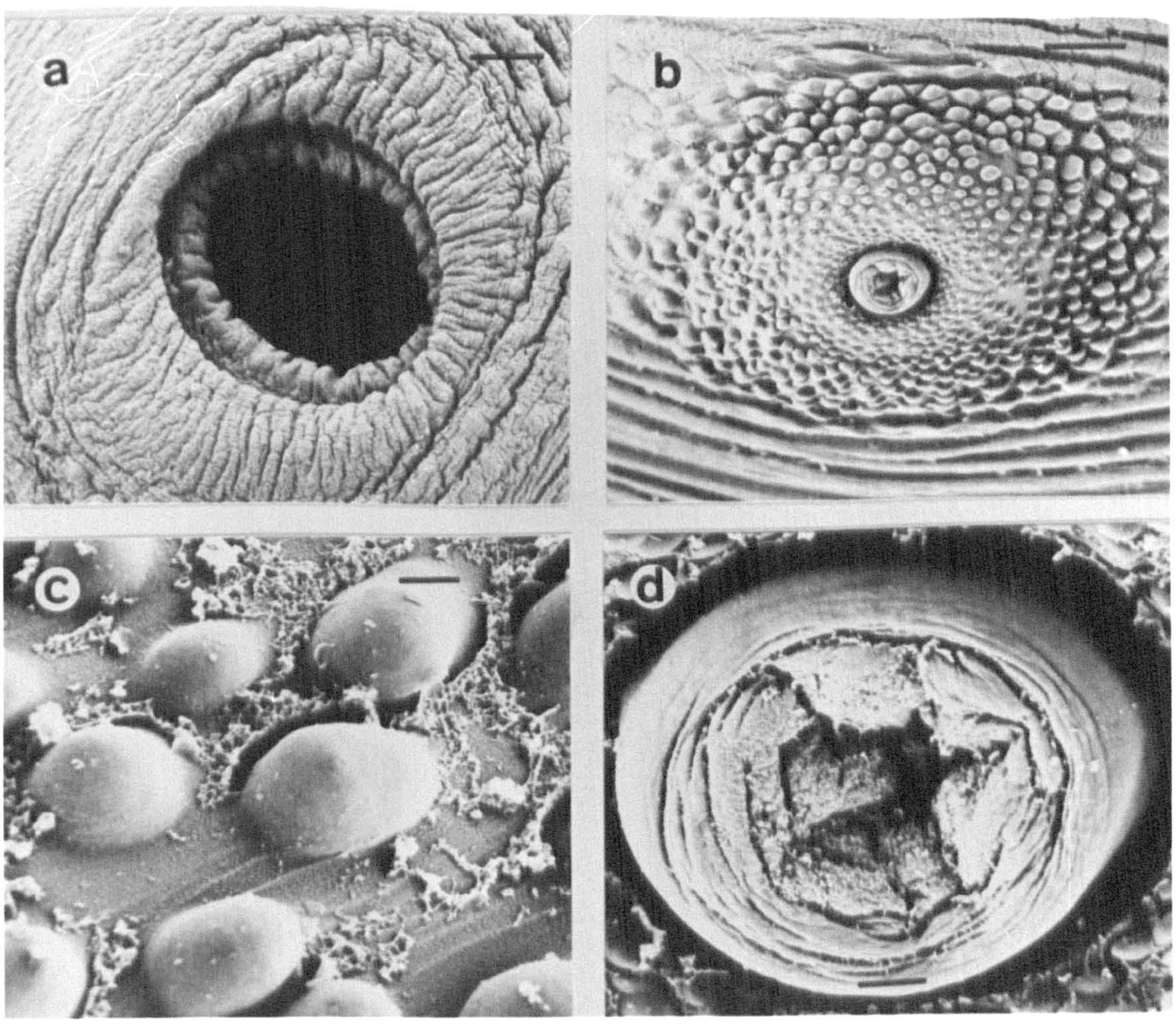

a
b
c
d

FIGURE 164

Stephanopharynx compactus Fischoeder, 1901

a. Whole worm, ventral view

b. Whole worm, sagittal view

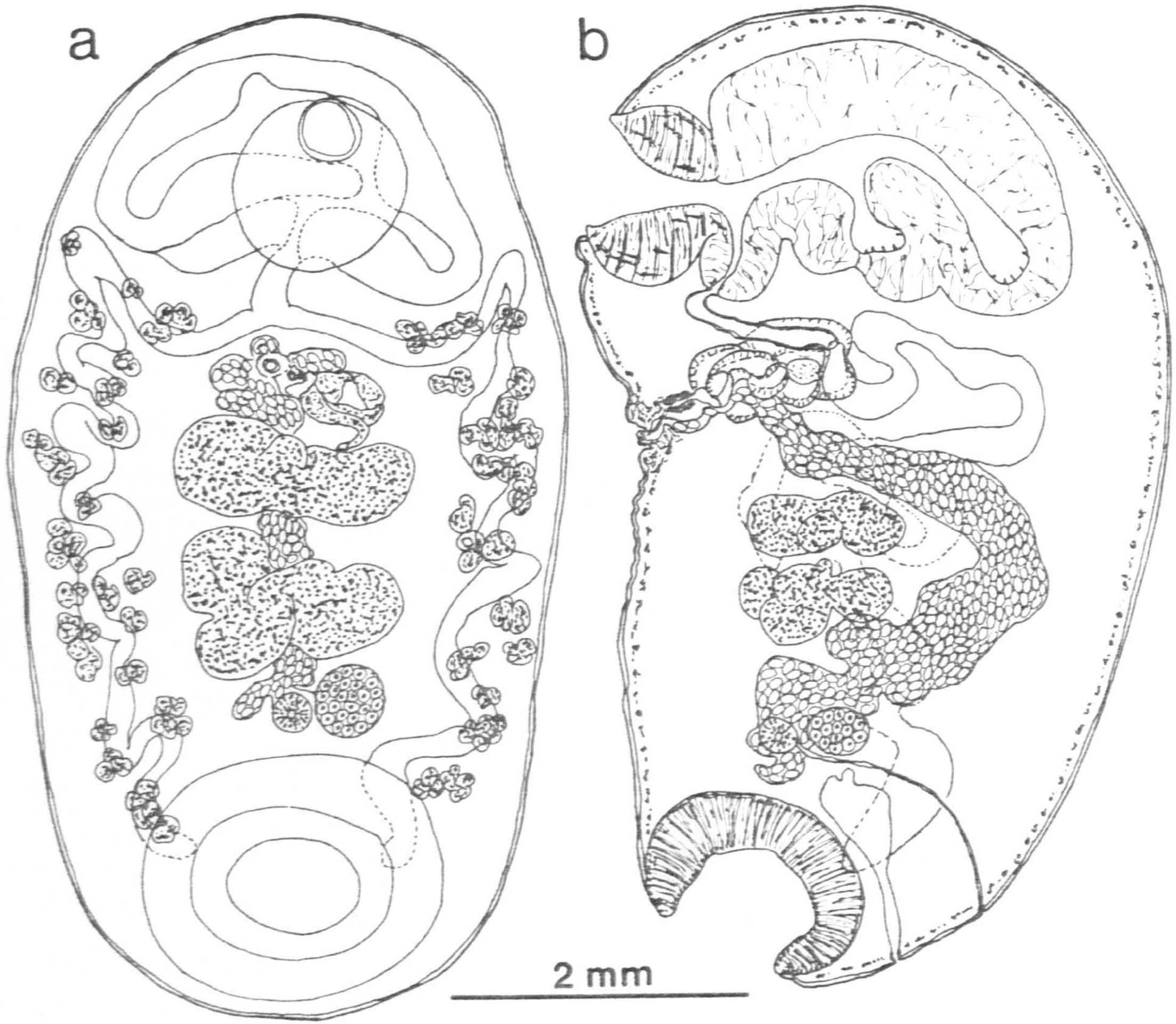

a
b
2 mm

FIGURE 165

Stephanopharynx compactus Fischoeder, 1901

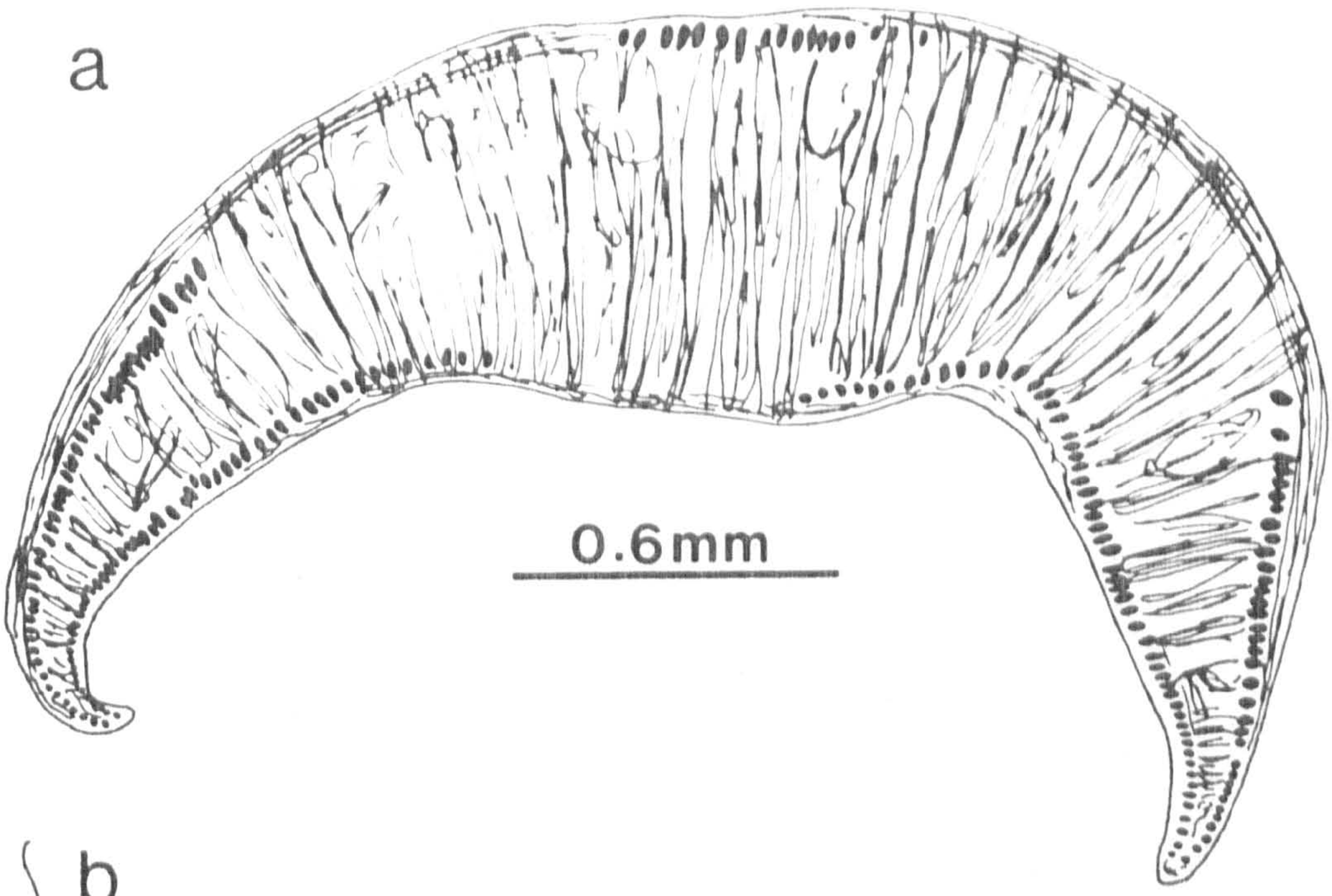
(median sagittal section)

a. Acetabulum (stephanopharynx type)

b. Oesophagus

c. Terminal genitalium (stephanopharynx type) and pars prostatica

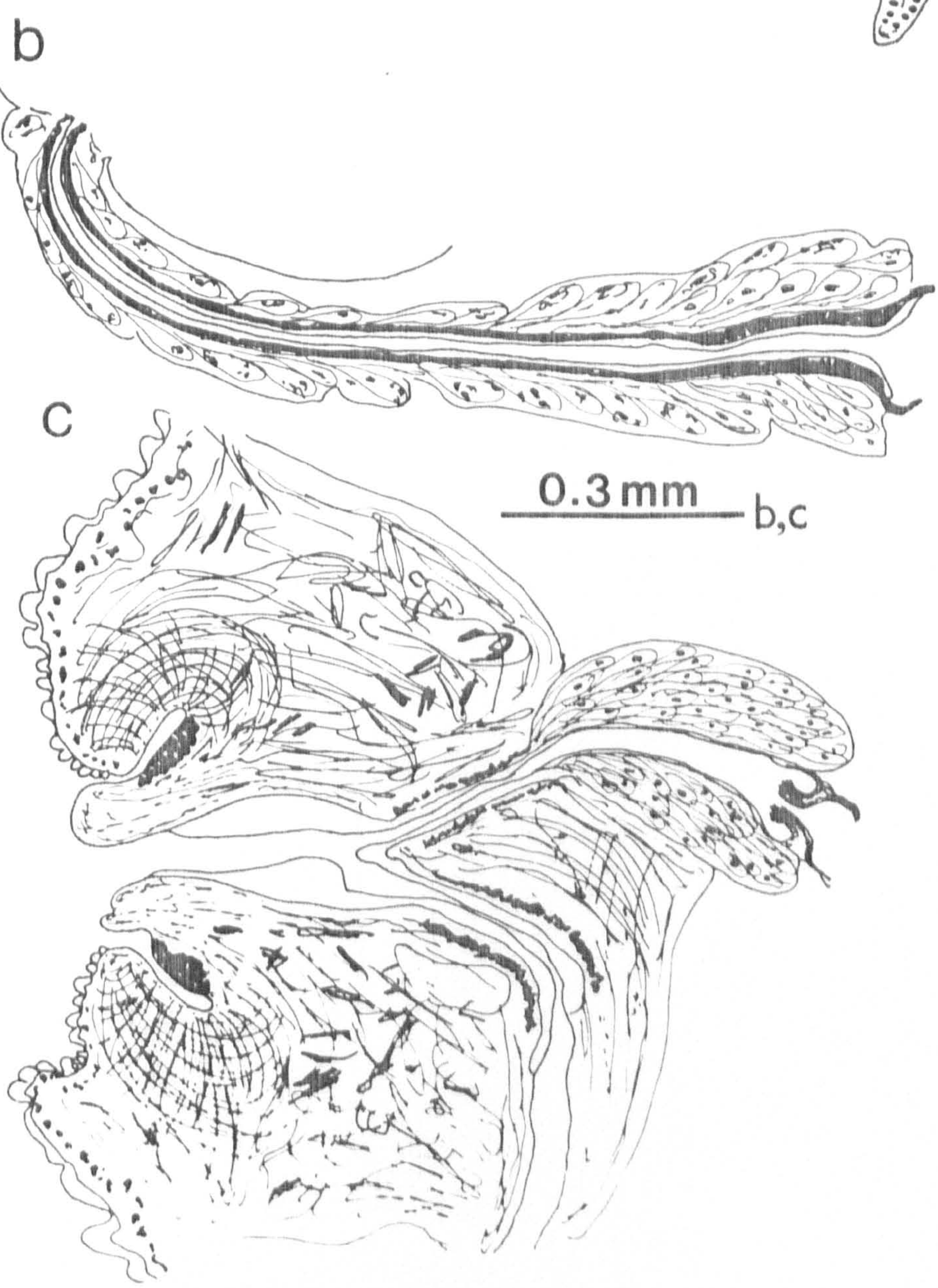
a



0.6mm

b

c



0.3mm b,c

FIGURE 166

Stephanopharynx compactus Fischoeder, 1901

Pharynx and showing the pharyngeal pouch or sac in two different planes of section

a. Median sagittal section

b. Lateral sagittal section, note long papillae on the internal surface of the pouch concentrated in this section

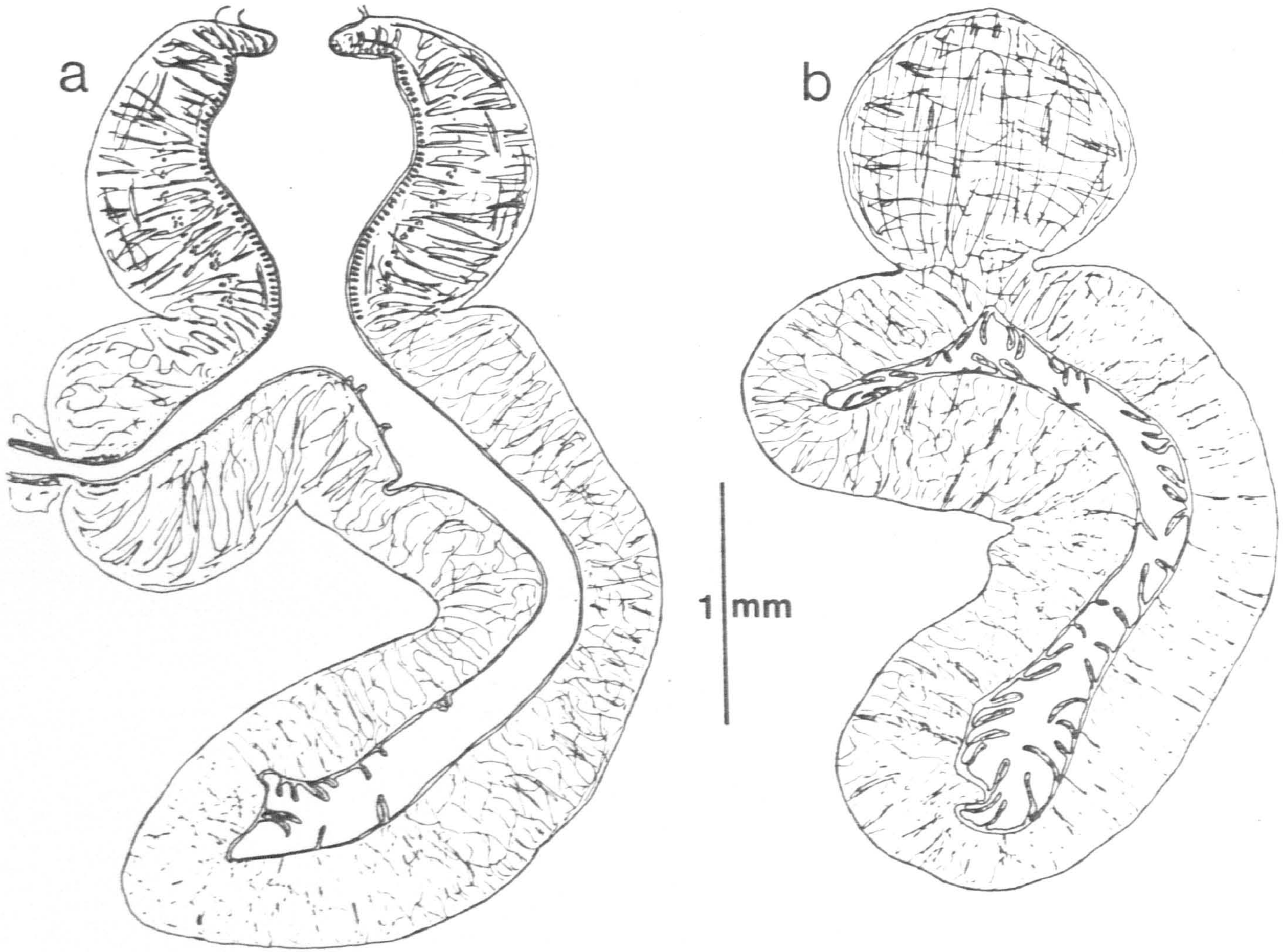

a
b
1 mm

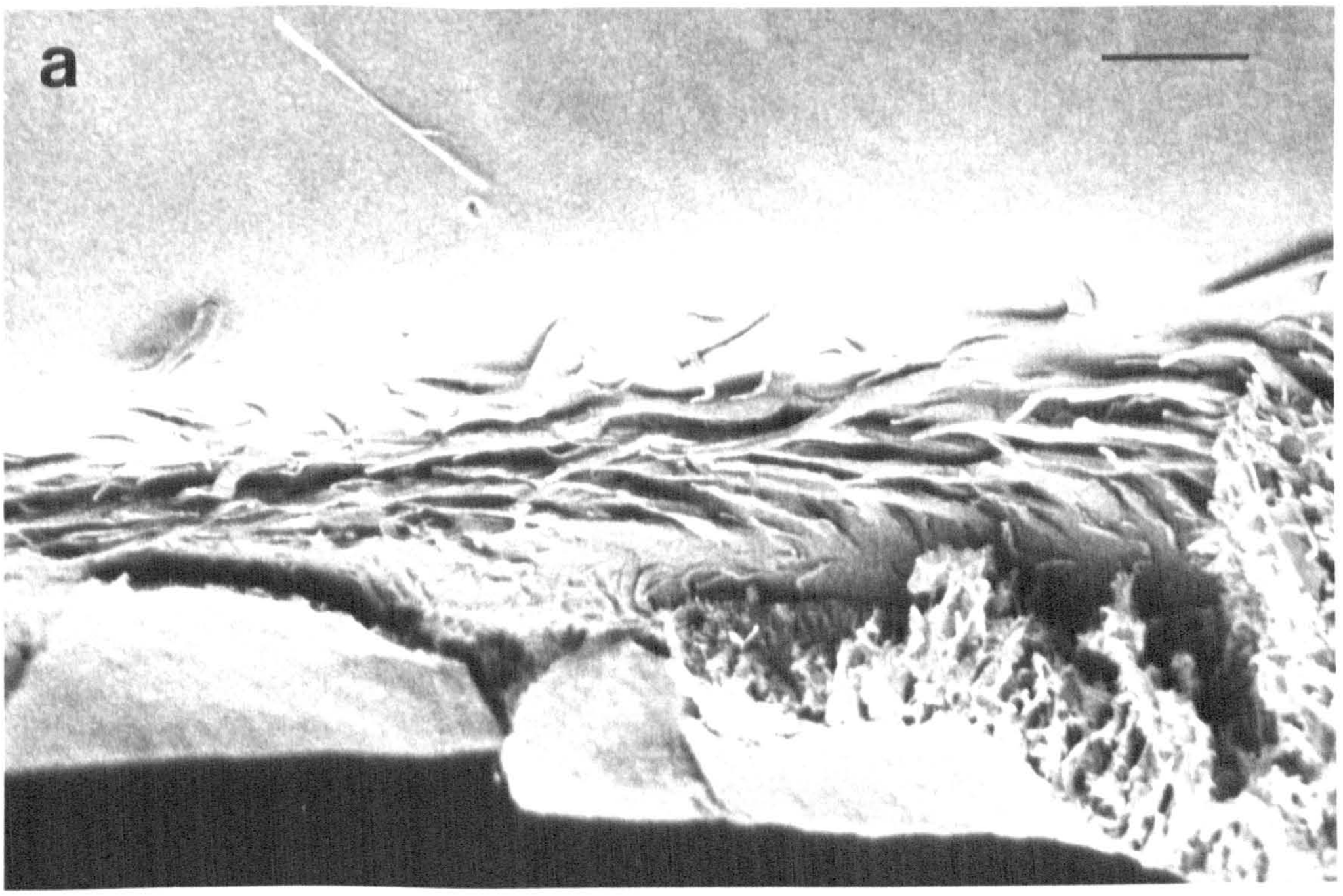
FIGURE 167

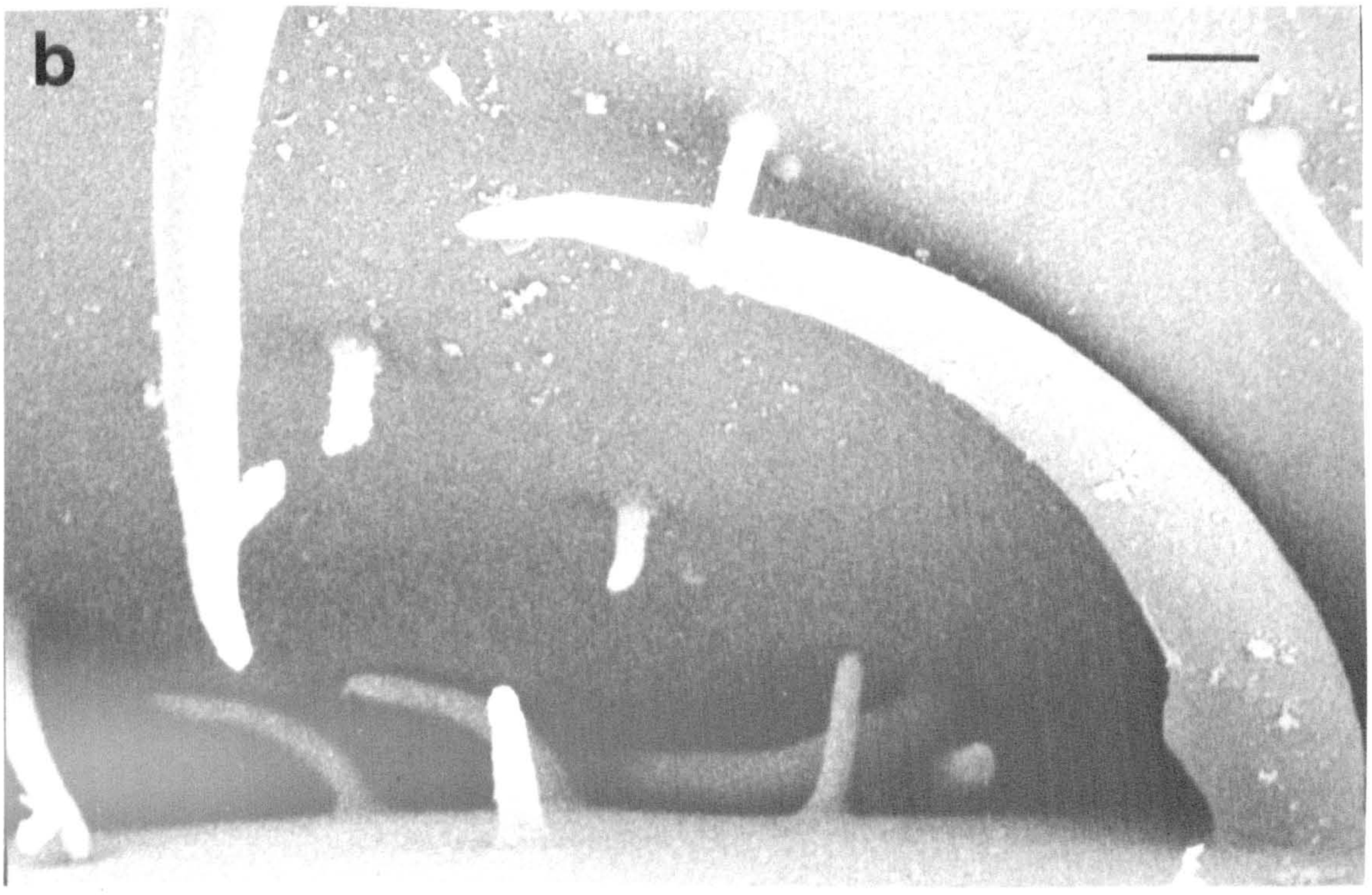
Stephanopharynx compactus Fischoeder, 1901

Internal surface of the pharyngeal pouch or sac (SEM)

a. General view showing the presence of long papillae concentrated only on the lateral corner of the pouch (scale bar = 100 µm)

b. Closer view of papillae, note long and slender shape (scale bar = 10 µm)


a


b

DISCUSSION

Fischoeder (1903) in his description of Stephanopharynx compactus made no mention of papillae lining the lumen of the pharyngeal diverticulum. In this study however, specimens examined from various hosts including those from the type host of the species revealed the presence of long and filiform-like papillae lining the lateral corners of the pharyngeal diverticulum. Because of their lateral location, they are not observed when median sections are only examined. Furthermore, they sometimes fall off when processing microscopic sections. It was found out that these papillae are best demonstrated in specimens which are stained as whole and later hand thick sectioned. Näsmark (1937) in his illustration of the pharyngeal diverticulum of the species in lateral sagittal section (Fig. 2) has clearly showed the presence of papillae. Fischoeder (1903) possibly failed to examine carefully the internal surface of the pharynx and its diverticulum and besides, he had only three specimens for study.

Stephanopharynx secundus was described by Stunkard (1929) as a new species based on only five young specimens from the stomach of Redunca bohor (=Redunca redunca) in the Belgian Congo (now Zaire). The species was separated from S. compactus only because of its larger size. As already explained elsewhere in this work, size among the paramphistomids vary considerably even in the same species and is affected by various factors among which is the host. Stunkard's material came from a host different from that of Fischoeder's. Of the five original specimens of Stunkard, only one was available and was loaned for re-examination from the American

Museum of Natural History, New York (Coll. No. 165). The specimen is in alcohol and unfortunately, no permission was granted to section it. The specimen however showed no distinct difference in form, shape and surface structures from specimens of S. compactus examined in this work. Stephanopharynx secundus Stunkard, 1929 is therefore regarded here as a junior synonym of S. compactus Fischoeder, 1901.

Stephanopharynx coilos from the stomach of Hippotragus equinus in the Belgian Congo (now Zaire) was established by Dollfus (1963) as a new species mainly on the basis of a large pharyngeal diverticulum and presence of filiform papillae in its lumen. As already shown earlier, such features are also those of S. compactus. The type specimens loaned from the Musée Royal de l'Afique Centrale, Tervuren were re-examined and these revealed that the species in question is identical in all respects with S. compactus and should be synonymized with it.

Stephanopharynx compactus is strictly African in distribution and has never been recorded outside the continent.

When Fischoeder (1901, 1902, 1903) erected the genus Stephanopharynx, he attached it to the subfamily Paramphistominae despite the presence of a pharyngeal diverticulum. Stiles and Goldberger (1910) however erected a new subfamily, the Stephanopharynginae to accommodate it and this has been accepted by most authors. Skrjabin (1949) elevated it to family rank as Stephanopharyngidae but this has found no acceptance among subsequent workers. The writer believes that there is no justification in erecting a separate family for the above species.

The genus Balanorchis Fischoeder, 1901

INTRODUCTION

The genus Balanorchis was established by Fischoeder (1901) for a single species which he described as new, Balanorchis anastrophus from Cervus dichotomus (now Blastocerus dichotomus) in Brazil. Since then no additional species has been described and the genus remains to date monotypic.

Fischoeder's description of the species, although complete as regards to gross morphological, lacks histological details. Subsequent descriptions that appeared in literature have been drawn from Fischoeder's descriptions. Näsmark (1937) had no material for examination, hence he was unable to characterized the pharynx, acetabulum and terminal genitalium of the species. Most recently, Velazquez-Maldonado (1976) described the species based on new material obtained from Bos taurus in Brazil but the description is very brief and lacks histological details.

Based on new material, the species is here redescribed and illustrated. Details of the tegumental surface as observed under the scanning electron microscope are also given.

SYNONYM: Verdunia Lahille and Joan, 1917

GENERIC DIAGNOSIS

Paramphistomidae, Balanorchiinae. Body small, conical, nearly round in cross section; ventral pouch absent. Acetabulum sub-terminal or nearly terminal. Pharynx with paired diverticula; oesophagus without bulb or posterior sphincter; caeca long, reach acetabulum. Testes unlobed, symmetrical and anterior to acetabulum.

Cirrus pouch present and protrusible. Ovary and Mehlis' gland dorsal and anterior to the testes or just level to their anterior borders; vitellaria in lateral fields; Laurer's canal does not cross the excretory vesicle or duct. Genital sucker and genital papilla absent. Parasitic in the stomach of ruminants.

Type and only species: Balanorchis anastrophus Fischoeder, 1901

Balanorchis anastrophus Fischoeder, 1901

Synonym: Verdunia tricoronata Lahille and Joan, 1917

TYPE SPECIMENS: Not available for examination

MATERIAL EXAMINED: Host, locality and donor/collection

Bos taurus	Mato Grosso, Brazil	Instituto Oswaldo Cruz (Rio de Janeiro) coll. no. 3778, presented by Dr. Delir Correa Gomes.

HABITAT: Rumen

DESCRIPTION:

Body small, conical, nearly round in cross section, 1.91-3.68 mm long, 1.01-1.35 mm in greatest width in the dorso-ventral direction. Body surface has tegumental papillae on the anterior end around the oral opening and on the posterior end around the acetabular opening. Those around the oral end consist of long finger-like structures measuring from 30 to 65 µm long and on the sides of which are smaller structures emanating as side branches measuring from 4 to 6 µm long each has a cilium on its tip. The same kind of small ciliated structures are also found on the surfaces between and around the long papillae. Those around the acetabular opening are small, dome-shaped and non-ciliated, measuring about 8-12 µm and are randomly arranged.

Acetabulum subterminal or nearly terminal, 0.40-0.58 mm in external diameter in the dorso-ventral direction; ratio to body length 1:3.5 to 1:4.5; of the streptocoelium type (sensu Näsmark, 1937) in median sagittal section but the circular muscle units are smaller in size than those in other species of the same type; number of circular muscle muscle units, d.e.c., 10-16;

d.i.c., 23-34; v.e.c., 18-24; v.i.c., 27-44; m.e.c., 10-14.

Pharynx 0.16-0.25 mm long, 0.20-0.23 mm in the dorso-ventral direction, with paired diverticula measuring 0.20-0.36 by 0.16-0.24 mm; ratio to body length 1:7.7 to 1:10, to the diameter of the acetabulum 1:1.7 to 1:2.9; of the balanorchis type (new type) in median sagittal section characterized by the presence of a paired diverticula, weakly developed and sometimes indistinct interior circular muscle units, absence of middle and exterior circular muscle units, weakly developed interior and exterior longitudinal muscle fibres, absence of lip, anterior and posterior sphincters and presence of relatively well developed radial muscle fibres. Oesophagus 0.53-1.30 mm long, usually bent dorsally; musculature of wall relatively thick, without bulb or posterior sphincter; lumen lined by hyaline layer throughout its length. Caeca in lateral sides of the body, form shallow dorso-ventral bends, reach level of acetabulum with their blind ends dorsally to it.

Testes unlobed, usually oval or elongate in the dorso-ventral direction, symmetrical in position in the posterior half of the body anterior to the acetabulum; right testis 0.35-0.48 mm long, 0.50-1.20 mm in the dorso-ventral direction; left testis 0.32-0.45 mm long, 0.48-1.10 mm in the dorso-ventral direction. Cirrus pouch present, large, 0.54-0.61 mm long, 0.25-0.34 mm wide, usually protrudes outside the body surface; pars prostatica absent; pars musculosa slightly coiled, thick walled and inside the cirrus pouch; seminal vesicle thin-walled, coiled and outside the cirrus pouch.

Ovary subspherical, 0.15-0.17 by 0.16-0.20 mm, anterior and dorsal to the testes; Mehlis' gland close to ovary, 0.10-0.13 by 0.10-0.17 mm; Laurer's canal does not cross the excretory vesicle or duct and opens on the dorsal surface anteriorly to the excretory pore; uterus runs forward in between the testes then ventral to the cirrus pouch; vitellaria in lateral fields, consist of large follicles, extend from level of oesophageal bifurcation to acetabulum, not confluent dorso-medially in their anterior or posterior limits; egg 124-138 by 73-80 µm.

Terminal genitalium of the balanorchis type (new type) in median sagittal section characterized by the absence of a genital papilla, presence of a cirrus pouch which is protrusible outside the body surface and the genital fold lacking circular muscle units but with relatively well developed radial muscle fibres.

Excretory vesicle relatively small, in between the testes and postero-ventral to the ovary and Mehlis' gland; excretory duct relatively long and its pore opens on the dorsal surface posteriorly to the Laurer's canal opening.

FIGURE 168

Balanorchis anastrophus Fischoeder, 1901

(SEM)

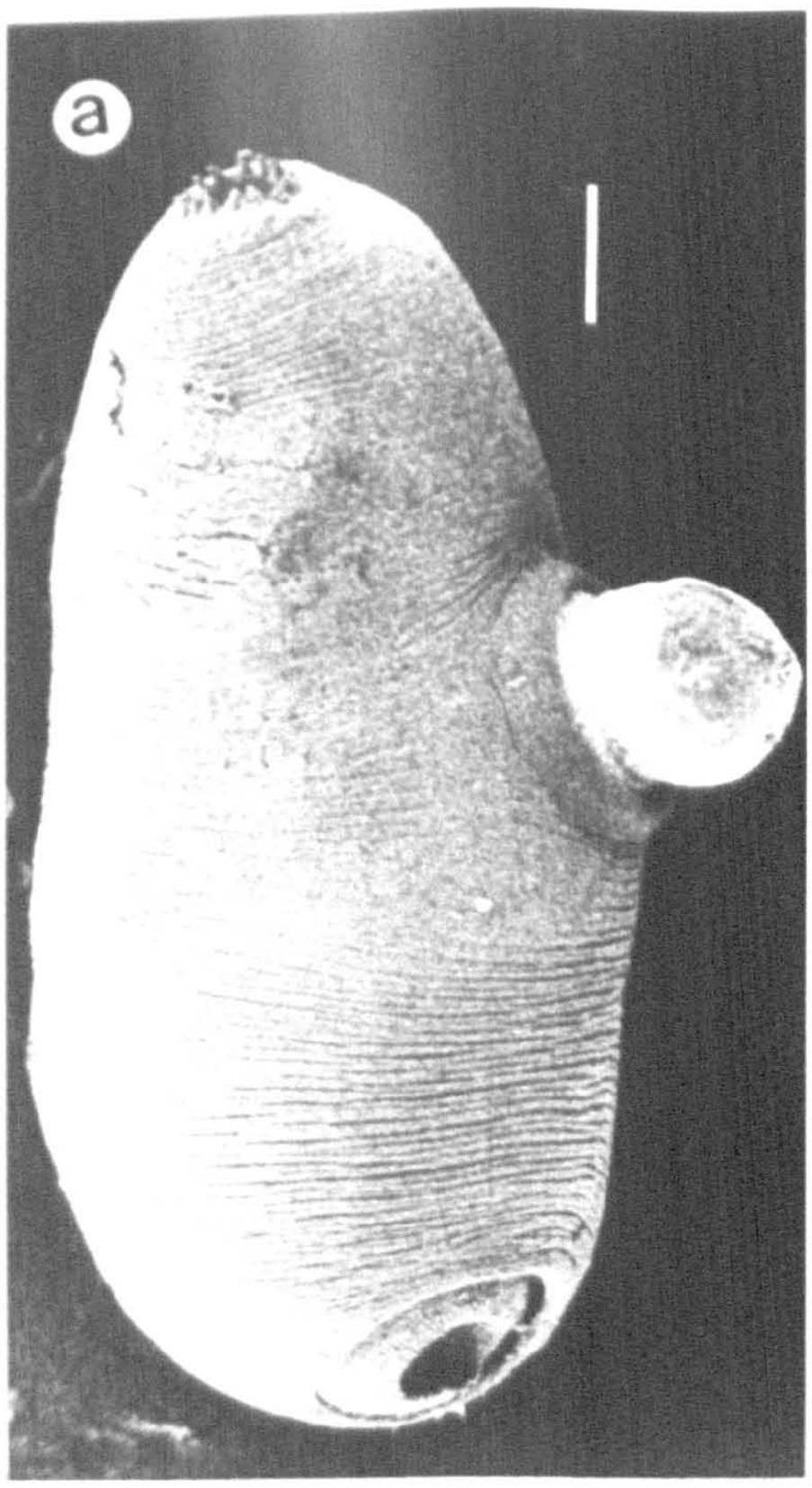
a. Whole worm, lateral view (scale bar = 200 µm)

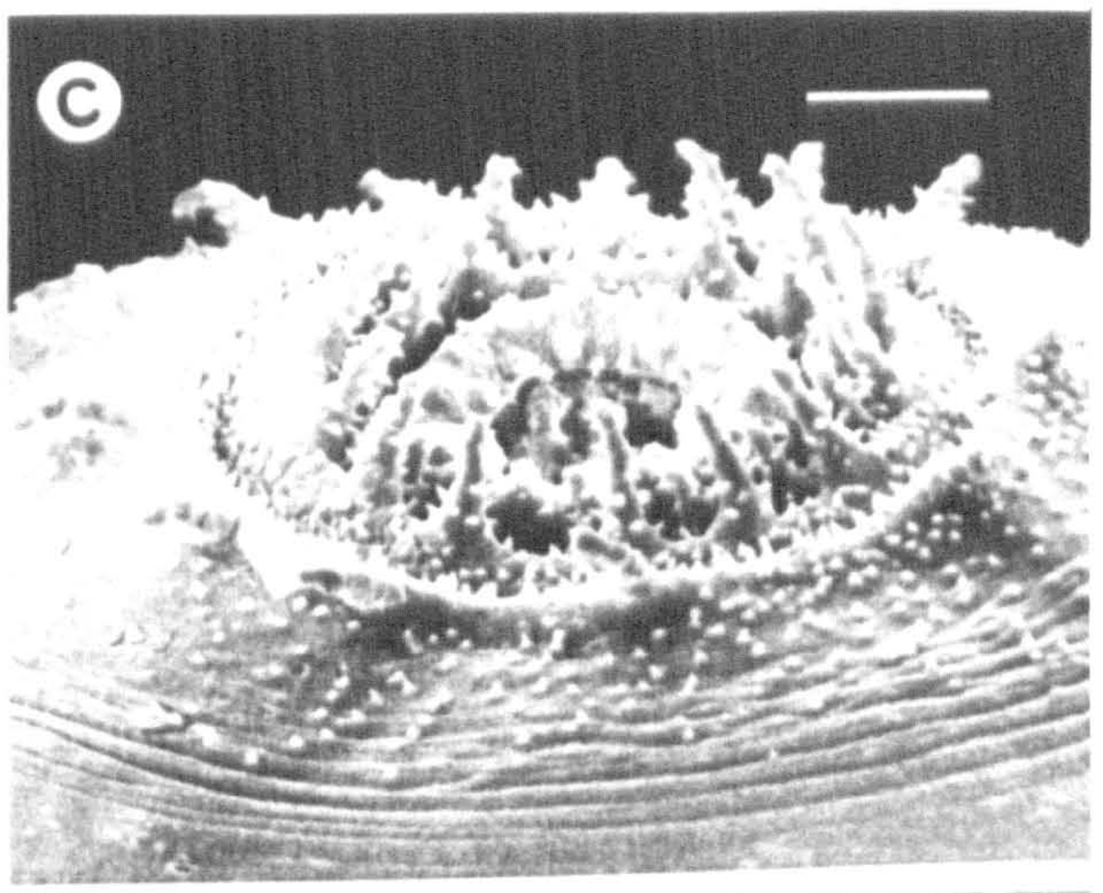
b. Acetabular region (scale bar = 50 µm)

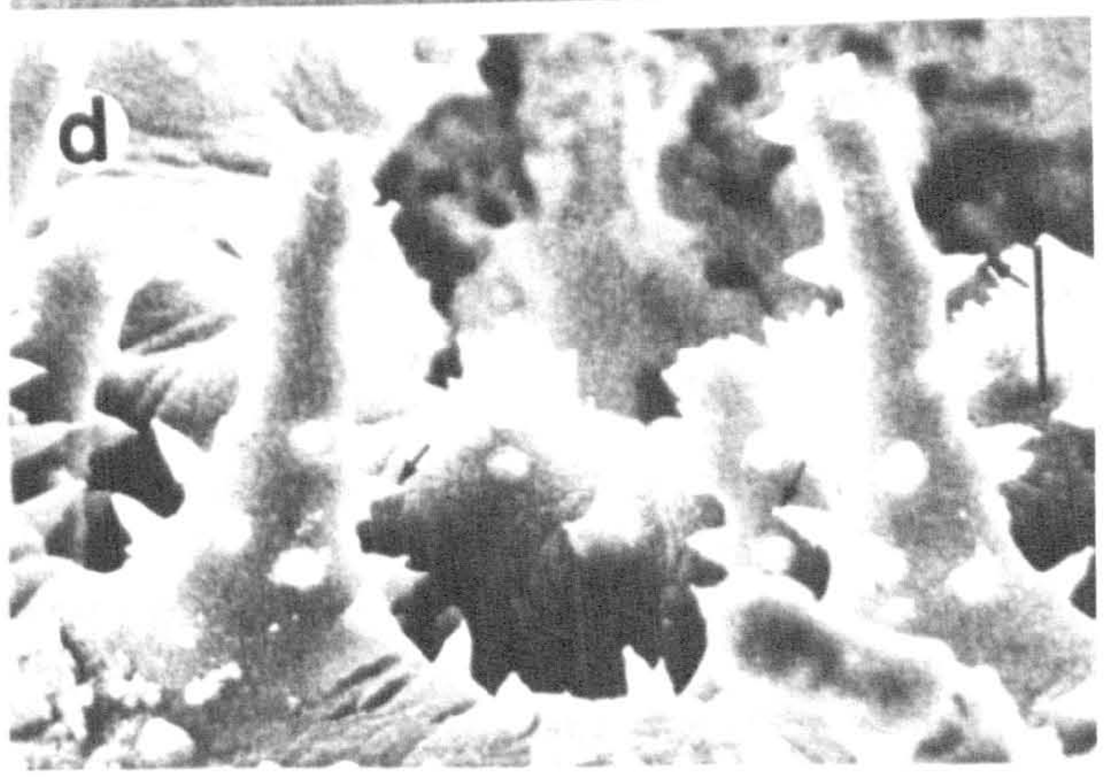
c. Anterior end, note long papillae around oral opening (scale bar = 50 µm)

d. Closer view of long papillae on anterior end, note short and uniciliated branches (scale bar = 10 µm)

e. Genital pore region with protruded cirrus pouch (scale bar = 10 µm)


a


c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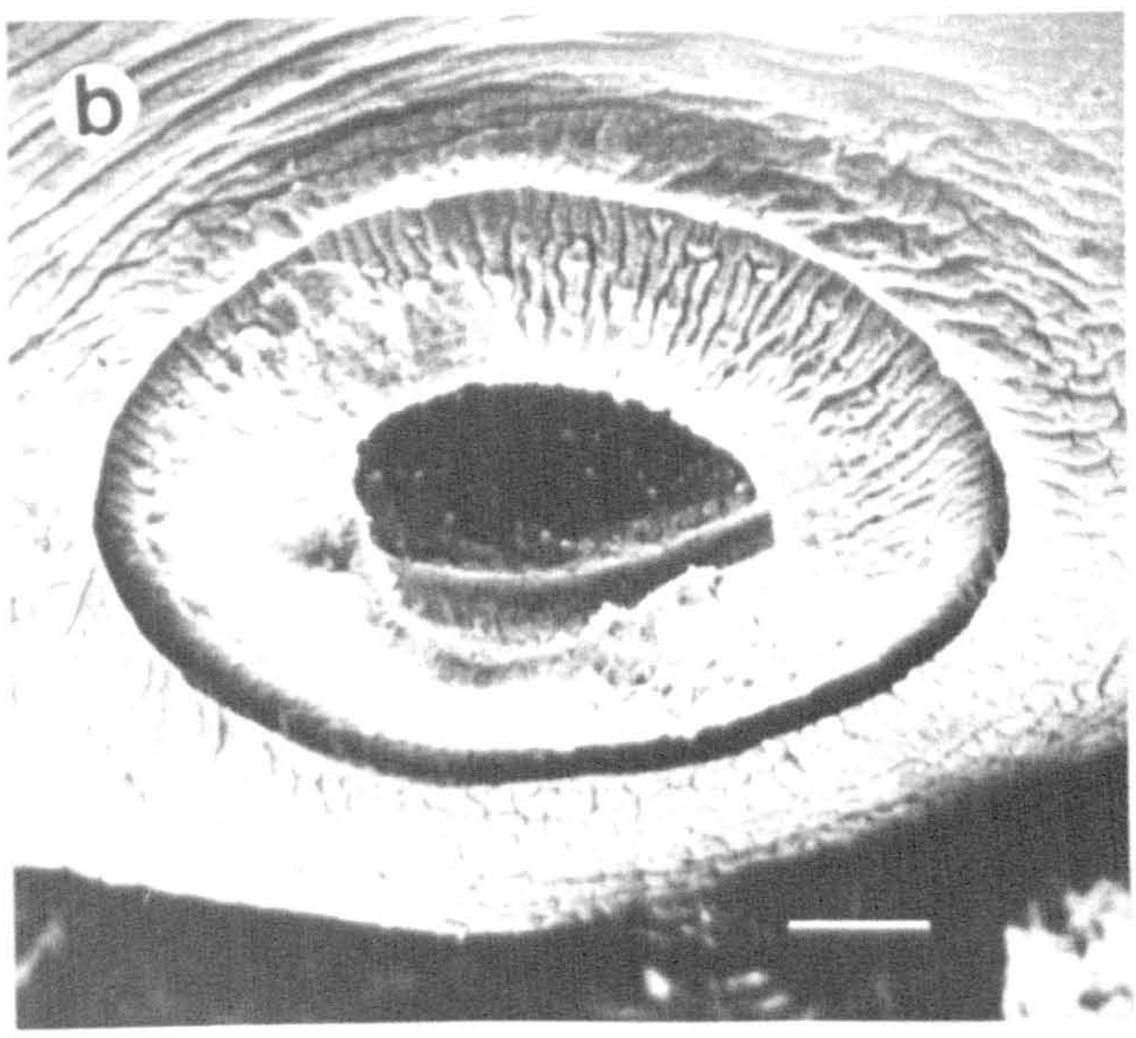
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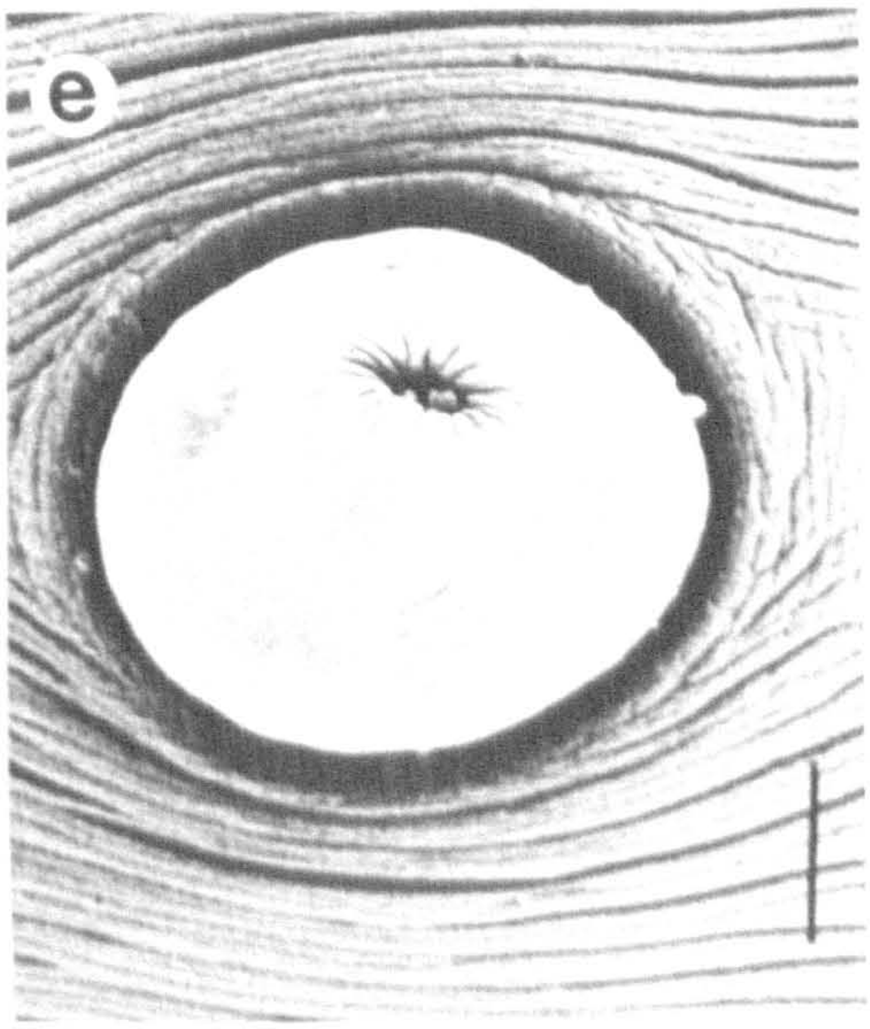

e

FIGURE 169

Balanorchis anastrophus Fischoeder, 1901

a. Whole worm, ventral view

b. Whole worm, sagittal view

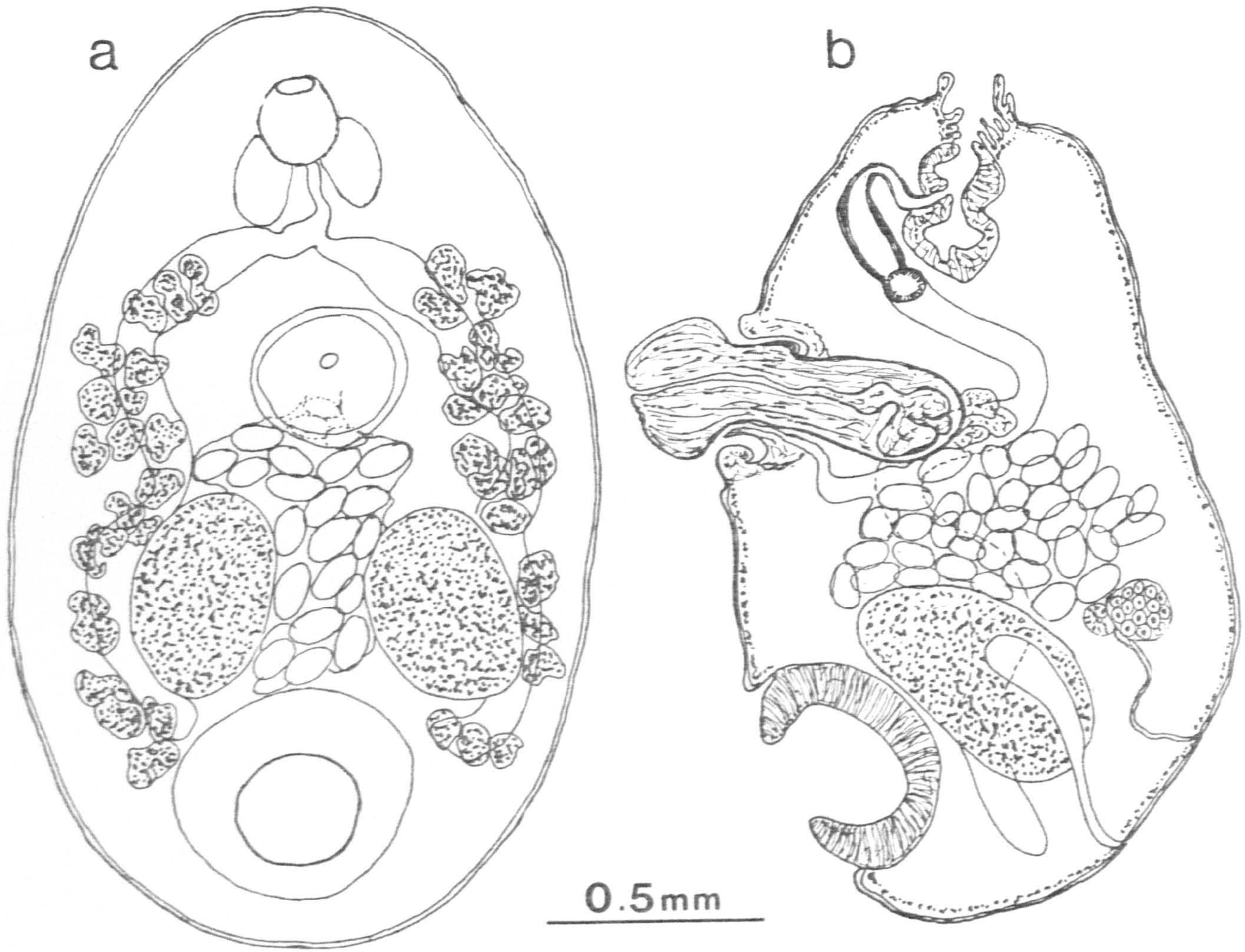

a
b
0.5mm

FIGURE 170

Balanorchis anastrophus Fischoeder, 1901

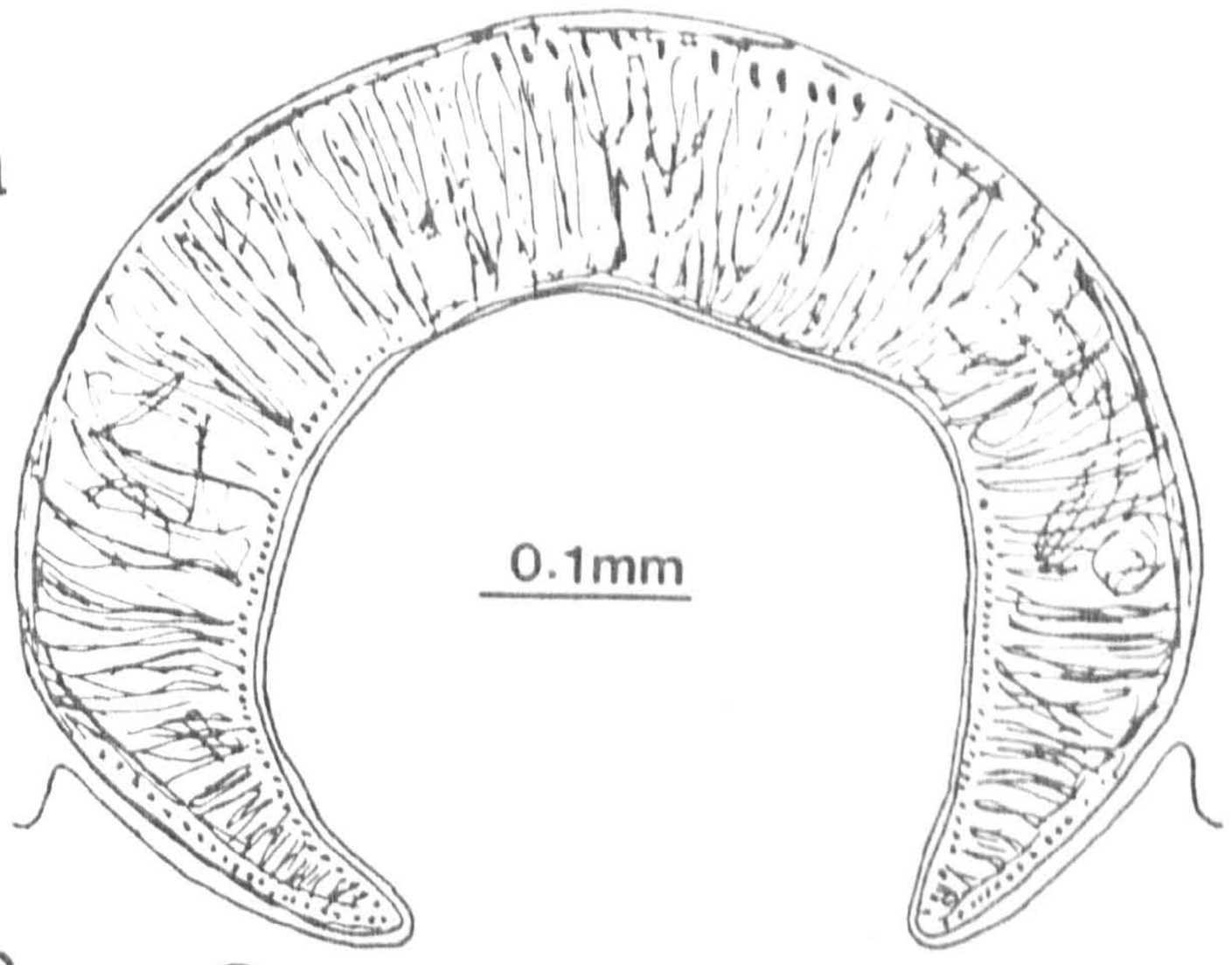
(median sagittal section)

a. Acetabulum (streptocoelium type)

b. Pharynx (balanorchis type) and oesophagus

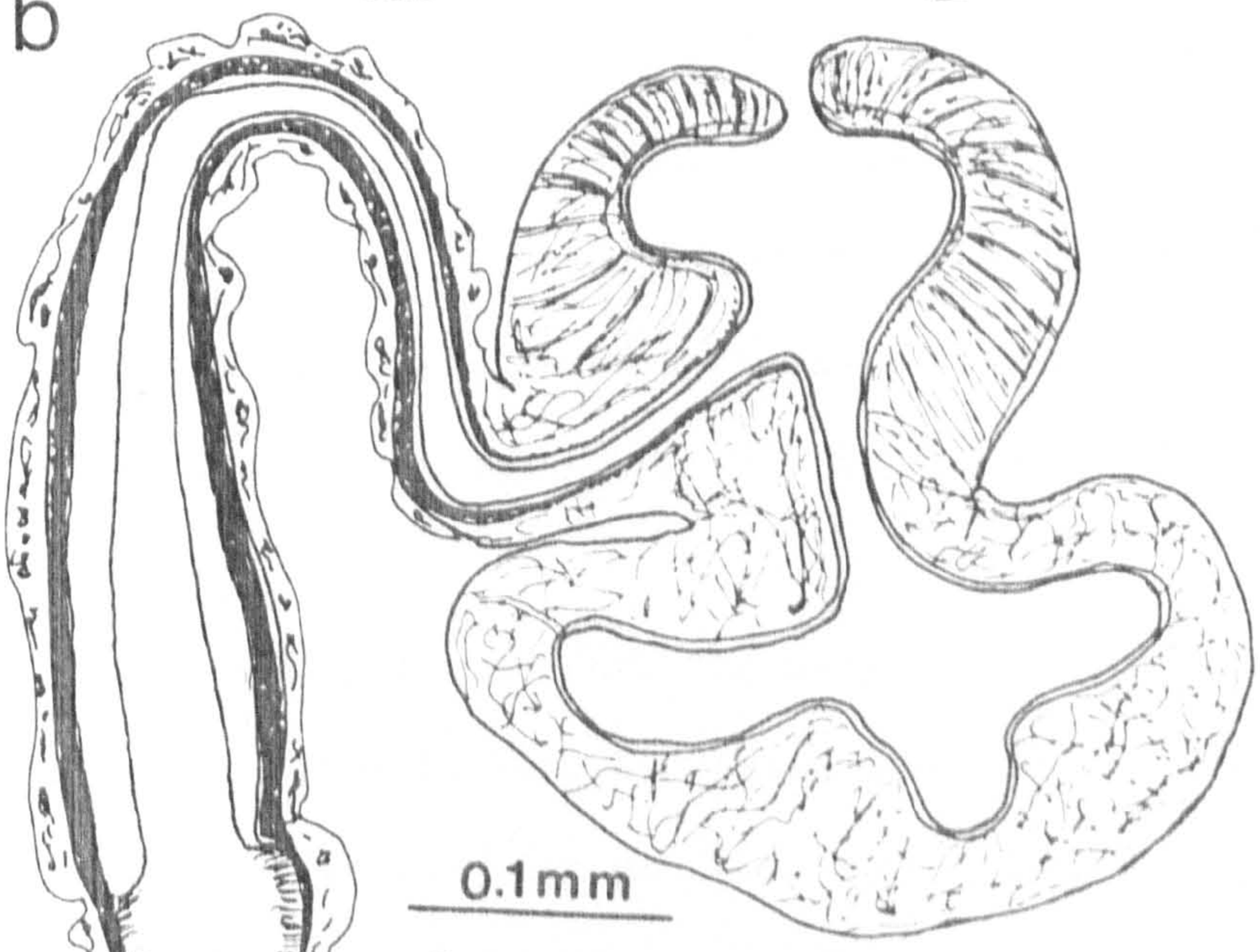
c. Terminal genitalium (balanorchis type)

a



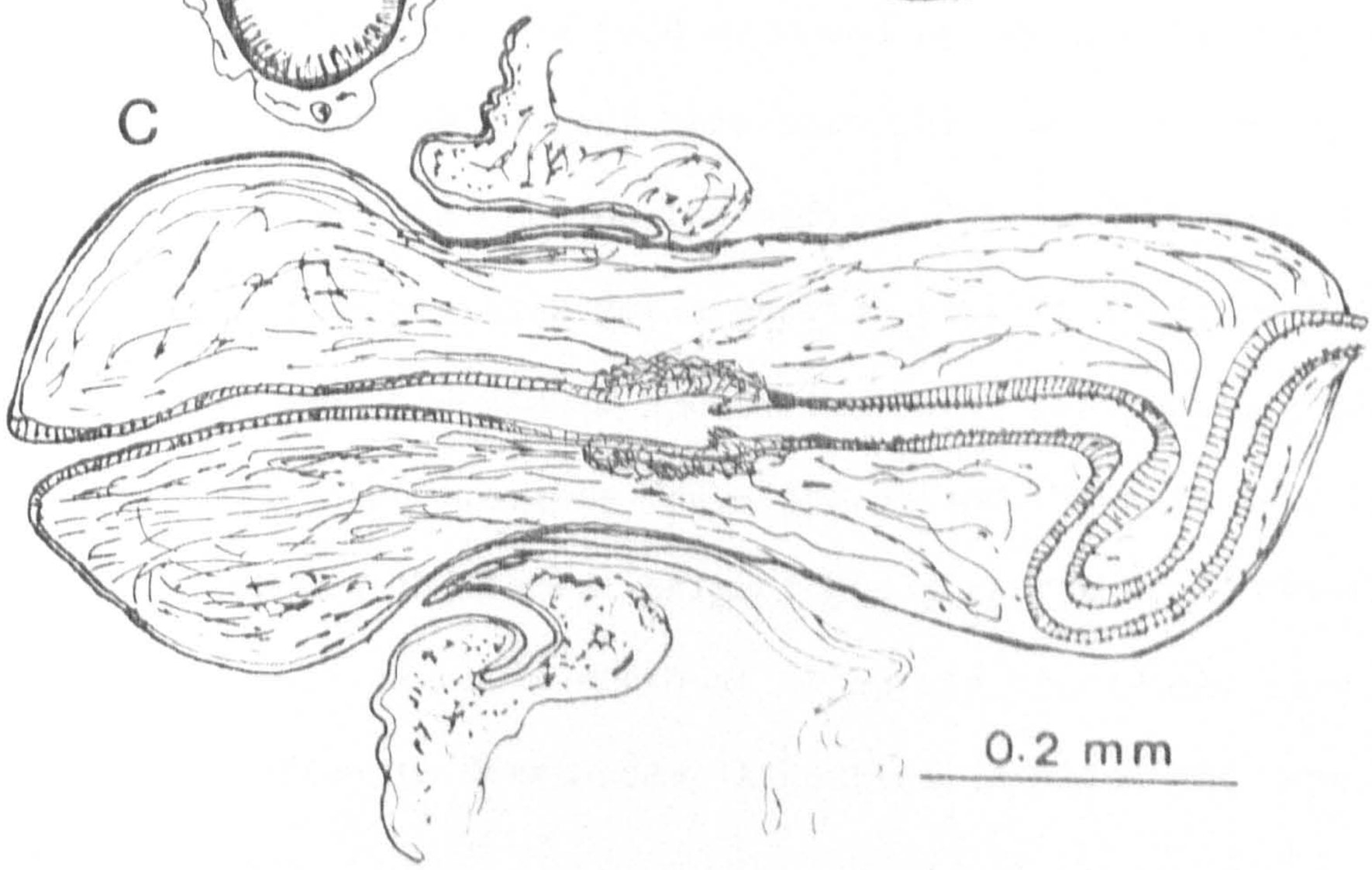
0.1mm

b



0.1mm

C



0.2 mm

DISCUSSION

The present description of the species provides for the first time histological features of the pharynx, acetabulum and terminal genitalium as seen in median sagittal section and gives an account of the distribution and details of tegumental papillae as observed under the scanning electron microscope. Previous descriptions of the species merely stated the presence of "long papillae" (Fischoeder, 1903; Valázquez-Maldonado, 1976) or "oral tentacles" (Szidat and Ostrowski de Núñez, 1962; Schiffo and Lombardero, 1974) and no details of these papillae were given nor the presence of other papillae around the acetabular opening was observed. Szidat and Ostrowski de Núñez (1962) mentioned the presence of "spines" on the "oral tentacles" and these were found in the presenct study as uniciliated structures emanating as side branches of the long anterior papillae.

Fischoeder (1903) stated that the genital pore in this species is surrounded by a muscle ring but examination of sagittal sections in this study revealed no circular muscle fibres but only radial muscle fibres on the fold surrounding the genital pore. It is also interesting to note here that the cirrus pouch in this species is protrusible outside the body surface and because of this, it could easily be mistaken for a genital papilla which is absent. All specimens examined showed the cirrus pouch protruding outside the body surface and previous descriptions and illustrations of the species showed the same. Balanorchis anastrophus has been reported as the cause of death of 24 cattle of various ages due to heavy infection in Corrientes, Argentina (Schiffo and Lombardero,

1974). The species appears to be restricted only to South America as it has never been reported outside the continent.

The name Verdunia tricoronata described by Lahille and Joan (1917) as a new genus and a new species has been shown by Travassos (1924) to be a junior synonym of Balanorchis anastrophus Fischoeder, 1901 and as a consequence, the genus Verdunia became a synonym of Balanorchis. This synonymy has been accepted by sybsequent workers.

When Fischoeder (1901, 1902, 1903) erected the genus Balanorchis, he was uncertain of its subfamily position. Stiles and Goldberger (1910) and Maplestone (1923) attached it to the Cladorchiinae Fischoeder, 1901. Stunkard (1925) however proposed the erection of a new subfamily to contain it, the Balanorchiinae. Although no diagnosis was given, the subfamily was generally accepted. Later, Yamaguti (1958, 1971) provided a diagnosis for the subfamily.

Zoogeographical affinities of paramphistomids of ruminants

To present an accurate picture of the distribution of any particular group of parasites is difficult to provide especially when there is a dearth of information and when existing information contains inaccurate records of species due to misidentifications. Such is the case for the paramphistomids of ruminants where our knowledge of their geographical distribution is far from complete, gaps exist in certain areas and the life history of many species remains unknown. The situation is confused by many previous inaccurate records including reports of species by some authors who followed synonymies which were later proved to be valid species. Some misidentifications have been established by re-examination of the original materials or analysis of the original descriptions and accompanying illustrations but others could not be verified particularly when these records are incomplete or when the original materials are no longer available for re-examination.

All nine species of the genus Paramphistomum are parasitic only in ruminants, the majority of which occur in Asia and Europe and few are restricted to certain areas elsewhere. The exact distribution of Paramphistomum cervi is difficult to assess due to many previous dubious records. Maplestone (1923) confused the situation by placing eight species as synonyms of P. cervi and some subsequent authors based their identifications on this synonymy. Thus, the species has been recorded in various parts of the world giving a picture of a worldwide distribution. However, seven of the eight synonyms (some now belong to other genera) are in fact

valid species. Therefore previous records of *P. cervi* which followed Maplestone's synonymy could also be any of the seven valid species. Subsequent re-examination of available original materials and investigation of recent collections have shown that the distribution of the species is not worldwide as was originally thought. Fischoeder (1903) was of the opinion that the species is purely of European distribution and Näsmark (1937) strongly endorsed this view. Dinnik and Dinnik (1954) have shown that what was previously recorded as *P. cervi* in East Africa by Dinnik (1951) was actually *P. microbothrium* (now moved to the genus *Calicophoron*). Record of the species by Joyeux and Baer (1928) in Dahomey and Stunkard (1929) in the Congo was regarded by Näsmark (1937) as dubious identifications. He considered Stunkard's material as *P. clavula* (now moved to the genus *Calicophoron*) and concluded that *P. cervi* does not exist in Africa south of the Sahara. Swart (1954) also claimed that previous records of *P. cervi* in the Republic of South Africa were in fact *P. microbothrium*. Looss (1912) stated that what he described as "*Amphistomum conicum*" (=*P. cervi*) in Egypt in 1896 was actually *P. microbothrium*. Sey did not find *P. cervi* in his examination of amphistomes from Egyptian ruminants and stated that previous records of the species in the country could be *P. microbothrium*. Round (1968) concluded that none of the records of *P. cervi* in Africa is likely to be that of the species but of related ones.

Durie (1951) has shown that previous records of *P. cervi* in *Australia* were erroneous and these actually consisted of two species, *Ceylonocotyle streptocoelium* (now *Orthocoelium streptocoelium*) and

Calicophoron calicophorum. Although P. cervi has been recorded in the Philippines (De Jesus, 1938; Tubangui, 1947), recent collections did not reveal the presence of this species there (Eduardo and Manuel, 1975; present work). Sey (1979) did not identify P. cervi in his examination of several collections of amphistomes of ruminants in India and specimens labeled "P. cervi" presented to him by various Indian authors were infact either P. epiclitum or P. gracile. He came to the conclusion that previous records of P. cervi in the subcontinent could either be one of the two other species. Caballero y Caballero, Brenes and Jiménez-Quirós (1959) recorded P. cervi from Bos taurus in San José, Costa Rica but their description and illustration clearly indicate that their specimen was Calicophoron microbothrioides.

The result of the present study which consisted of examination of several collections from various parts of the world, both early and recent collections, also strongly indicates a limited distribution of P. cervi. The species was identified only in collections from some countries in Europe and from the only two samples from the yak (Bos grunniens) in Tibet. Recently, Velazquez-Maldonado (1976) recorded the species from cattle in Rio Grande du Sul, Brazil. The intermediate host of P. cervi in nature in Europe is Planorbis planorbis (Szidat, 1936). The distribution of this snail host includes Europe and western and northern Asia (Ellis, 1969; Frandsen personal communication). Other snails which were found experimentally to serve as intermediate hosts are Anisus vortex, A. leucostomus, Bathyomphalus contortus,

Hippeutis complanatus, Armiger crista and Segmentina nitida (Kraneburg, 1977; Odening Bockhardt and Gräfner, 1978). Since many previous records of P. cervi in tropical regions were found to be cases of misidentifications and true records include only those in the north temperate regions, the species apparently is primarily a north temperate species and its distribution coincides with that of the intermediate host. Its introduction to south temperate areas is limited by the presence of suitable intermediate hosts as the species does not occur in South Africa and temperate parts of Australia but is now present in temperate parts of Brazil.

Two species namely, P. leydeni and P. hiberniae which are closely related to P. cervi are also of European distribution. The former species has been recently recorded in Rio Grande du Sul, Brazil (Velázquez-Maldonado, 1976). The known snail hosts of both species serve also as intermediate hosts for P. cervi. P. gracile, P. epiclitum, P. ichikawai and P. gotoi are primarily Asiatic species. The last two however extend to eastern Europe. P. ichikawai also occurs in Australia and P. gotoi has been recorded recently in Egypt from water buffalo (Sey, 1977). Both species and P. gracile have been recorded in Brazil (Velázquez-Maldonado, 1976) but the author's descriptions and illustrations clearly indicate that he was dealing with specimens of P. leydeni and P. cervi respectively. The known intermediate host of P. epiclitum is Indoplanorbis exustus whose distribution includes India, Thailand, Malay Peninsula and Sumatra (Malek and Cheng, 1974). The record of the presence of Cotylophoron indicum, a species regarded here as a synonym of P. epiclitum, in Africa by Näsmark

(1937) and Dinnik, Walker, Barnett and Brocklesby (1963) was a case of misidentification. The writer has re-examined Näsmark's material and his specimen was not of that species. Dinnik, Walker, Barnett and Brocklesby (1963) based their identification on Näsmark's description. The snail hosts of P. ichikawai are Segnitilia (now Helicorbis) alphena in Australia, Helicorbis sujfunensis, Gyraulus filiaris, Segmentina nitida, Polypylis largillieri and Hippeutis complanatus in the U.S.S.R. and Planorbis planorbis in Hungary (Durie, 1953; Kiselev, 1967 and Sey and Vishnyakov, 1976).

Paramphistomum liorchis is so far known only in North and South America. It is mainly a parasite of American deer belonging to the tribe Odocoelieini and its intermediate host is still not known. Only one species of the genus, P. cephalophi n. sp. is so far known in Africa and it is a parasite of the black-fronted duiker (Cephalophus nigrifrons), whose present distribution is restricted only to Central Africa.

As judged from these records, the genus Paramphistomum is predominantly Euroasian and the genus has probably developed and radiated from this region. Despite extensive movements of the final hosts, species of the genus have not been widely dispersed by them because their establishment in new environments depends on the presence of suitable intermediate hosts.

The genus Calicophoron is predominantly African and of the 12 species of the genus only four, namely C. calicophorum, C. papillosum, C. papilligerum and C. microbothrioides, do not

occur in Africa. All 12 species are restricted to the Bovidae. C. calicophorum is the most widespread species of the genus, occurring in Asia, the U.S.S.R. and Australia. Previous records of its occurrence in Africa are doubtful and probably are misidentifications. The description and illustration of Swart (1954) for the species based on specimens from the Republic of South Africa clearly indicate that his specimens were Calicophoron raja. Specimens labeled "Paramphistomum calicophorum" from the collection of the Onderstepoort Veterinary Research Institute were examined by the writer and these were found to be C. raja. Despite examination of extensive collections of amphistomes from various hosts and localities in Africa, C. calicophorum was not identified. The known intermediate hosts of C. calicophorum are planorbid snails, Pygmanisus pelorius, Glyptanisus (now Gyraulus) gilberti and Segnitilia (now Helicorbis) alphena in Australia (Durie, 1956) and Planorbis planorbis and Anisus sp. in the U.S.S.R. (Katkov, 1973; Khaidarov, 1974). The species has probably been introduced to Australia through importation of water buffalo at various times from Indonesia and India. Calicophoron papillosum and C. papilligerum are so far known in India and the former also in Indonesia and their snail hosts are still unknown. The genus Calicophoron is represented by only one species, C. microbothrioides in North and Central America including the Carribean. The snail hosts of this species in the U.S.A. are lymnaeids, Fossaria parva, F. modicella and Stagnicola cubensis. C. microbothrioides also occurs in Eastern Europe. It has been recorded in the U.S.S.R. as "Ceylonocotyle petrovi" (Davydova, 1961) and has been introduced

to Bulgaria through importation of cattle from the U.S.A. (Kamburov, Vasilev, Samnaliev and Kanev, 1977; Samnaliev, 1980). However, previous records of its occurrence in Albania (Erhardova, 1964) and Hungary (Kotlán, 1958, 1960) were cases of misidentifications and these authors were dealing with specimens of Calicophoron daubneyi (Odening and Gräfner, 1979).

The African species of Calicophoron are: C. microbothrium, C. bothriophoron, C. raja, C. clavula, C. sukari, C. phillerouxi, C. daubneyi and C. sukumum. Two of the above, namely C. microbothrium and C. daubneyi extend outside the continent. The former occurs in the Mediterrenean where it is the predominant species, in Portugal and in the Near East and the latter also in the Mediterrenean and Eastern Europe. The known intermediate hosts of C. microbothrium are bulinid snails. According to Dinnik (1965), Bulinus truncatus acts as the intermediate host for the species in North Africa, the Mediterrenean and the Near East and Bulinus tropicus and some species of the subgenus Physopsis in Africa south of the Sahara where these are widespread. On the other hand, the intermediate hosts of C. daubneyi are lymnaeid snails, Lymnaea truncatula in Kenya (Dinnik, 1962), L. truncatula and L. peregra in East Germany (Odening, Bockhardt and Gräfner, 1978) and L. peregra in Hungary (Sey, 1974). Dinnik (1962) has demonstrated experimentally that C. daubneyi failed to develop in bulinid snails which are intermediate hosts of C. microbothrium, likewise, the latter species failed to develop in Lymnaea truncatula which is the intermediate host of C. daubneyi. Sey (1974) failed to infect snails belonging to the same family as Bulinus, namely Planorbis

planorbis, P. spirorbis and Gyraulus crista with miracidia of C. daubneyi. Both species appear to be strictly specific to their respective intermediate hosts. Although C. microbothrium has been previously recorded in Eastern Europe, i.e. Hungary (Kotlán, 1958; Sey, 1971), Bulgaria (Mereminskii and Vishnyakov, 1969; Vasilev and Samnaliev, 1974; Mikhailova, Gateva and Nedeva, 1972-73), the Balkans (Kotrlá, Prokopič and Vishnyakov, 1974), recent investigations in these areas did not reveal the species but of another closely related one, C. daubneyi (Sey, 1974; Sey and Vishnyakov, 1976) and it is more likely that the above authors were dealing with the latter species. This is supported by the fact that bulinid snails which serve as intermediate hosts for C. microbothrium do not exist in these areas, but lymnaeid snails which are intermediate hosts of C. daubneyi are present. In Europe, bulinid snails are distributed only in the south-western areas which include the Iberian Peninsula, southern France, Sardinia and Corsica (Haas, 1935; Mandahl-Barth, 1965). Calicophoron raja has been recorded in 14 host genera all belonging to the Bovidae, 9 of which are solely African. This species is one of the commonest in Africa but its intermediate host still remains unknown. Recently, the writer has identified the species in a collection of paramphistomes from cattle in Cuba. It probably has been introduced through importation of cattle or other wild ruminants from Africa and has established itself in the island due to the favourable climatic condition and presence of suitable snail hosts. C. bothriophoron has also been recorded in the neighbouring islands of Madagascar and Mauritius in domestic ruminants, it has been probably introduced from Africa

through these hosts. The report of its occurrence in Bos taurus brachyceros in Bulgaria by Mikhailova, Gateva and Nedeva (1972-73) was a case of misidentification according to Odening and Gräfner (1979) who claimed that they were dealing with specimens of Paramphistomum ichikawai. C. clavula has been recorded in 8 host genera, all of the Bovidae, of which 5 are solely African wild ruminants. Its intermediate host in Somalia is Bulinus abyssinicus (Sobrero, 1962). Previous records of its occurrence in Hungary (Kotlán, 1958), Turkey (Güralp and Oguz, 1967) and Bulgaria (Mikhailova, Gateva and Nedeva, 1972-73) were misidentifications according to Odening and Gräfner (1979) and the species involved was in fact C. daubneyi. C. phillerouxi has been recorded in 8 host genera and with the exception of the genus Bos, all are solely African. Morphologically, the species is very closely related to C. microbothrium and could easily be mistaken for it. Dinnik (1961) has however demonstrated experimentally that the species does not develop in snail hosts which serve as intermediate hosts for C. microbothrium and C. daubneyi. Its known intermediate hosts are bulinid snails of the forskalii group (Bulinus forskalii, B. senegalensis and B. cernicus). C. sukari primarily occurs in domestic ruminants, but it has been recorded in Syncerus caffer and an unidentified antelope (Grétillat, 1964b). Its known snail host is Biomphalaria pfeifferi and its subspecies (Dinnik, 1954; Dinnik, 1965; Dinnik and Dinnik, 1957).

From the above, the genus Calicophoron appears to have developed in Africa and from here radiated to other areas. It is

also apparent that in species where the life cycle is known, many are highly specific to their snail hosts and their introduction to new environments is limited by the presence in nature of these intermediate hosts.

The genus Gigantocotyle is represented in Africa by three species, G. gigantocotyle, G. duplicitestorum and G. symmeri and in Asia by only one, G. formosanum. The first two species occur in the hippopotamus and the last two in ruminants. Round (1968) cited LeRoux (1933) to have recorded G. formosanum in cattle and Kobus leche in Zambia but this record has never been confirmed. As no additional record of this species in Africa has appeared since then despite extensive surveys in recent years, it is more likely that LeRoux was dealing with a different species. Although existing hippopotamuses are restricted to Africa, their fossil remains were found in Eurasia from the late Pliocene and Pleistocene periods and in Madagascar from the Pleistocene.

All three species of the genus Explanatum are Asian, previous records of the presence of E. explanatum in Africa (Maplestone, 1923; Dubois, 1930; LeRoux, 1931) were misidentifications. It is clear from the illustrations of Maplestone (1923) and Dubois (1930) that they were dealing with a different species, most likely Calicophoron raja. Jansen, Pačenovský and Krupicer (1974) recently reported the species from a Damaliscus albifrons that died in Rotterdam Zoo (although the origin of the host was not specified, it is an African host), but their illustration also clearly indicates that their specimen was C. raja. The known intermediate hosts of E. explanatum are: Indoplanorbis exustus, Gyraulus convexiusculus

and Lymnaea luteola f. australis (Srivastava, 1944; Singh, 1958; Mukherjee, 1962; Agrawal, 1971). Gyraulus convexiusculus also serves as intermediate host for E. bathycotyle (Jain, 1969) in India.

Members of the genus Cotylophoron occur in Africa, Asia and North and South America. Of the four African species, two were also recorded outside the continent, C. cotylophorum in various areas in Asia and North America and C. fuelleborni in the U.S.A. as C. noveboracensis. Some earlier records of C. cotylophorum however were misidentifications. C. cotylophorum of LeRoux (1930) in the Republic of South Africa and of Krull (1934) and Bennett (1936, 1938) in the U.S.A. were found to be Calicophoron microbothrium and C. microbothrioides respectively (Dinnik, 1965; Price and McIntosh, 1944). The writer has also examined specimens labeled "Cotylophoron cotylophorum" from Puerto Rico and these were found to be Calicophoron microbothrioides. Cotylophoron panamensis is the common species of the genus in the new world. Its distribution includes the southern states of the U.S.A., Central America and the Caribbean and northern regions of South America. Asian species of the genus include C. bareilliense in India and the Philippines and C. xiangjiangense in China. The genus does not occur in Europe and Australia despite extensive movements of animal hosts. Previous records of Cotylophoron species in Australia, Europe including the U.S.S.R. were misidentifications. The known intermediate host of C. cotylophorum in India is Indoplanorbis exustus (Srivastava, 1937; Sinha, 1950).

All the 11 species of the genus Orthocoelium have been reported from Asia and only two species have been recorded also outside the continent, O. streptocoelium in Australia (Durie, 1951) and the Belgian Congo (now Zaire) (Van Strydonck, 1970) and O. scoliocoelium in Kenya (Dinnik, 1956) and Chad (present work). These species have probably been introduced through the zebu cattle and water buffallo (Bubalus bubalis) from neighbouring Asian countries. Erhardova (1964) recorded O. scoliocoelium in Czechoslovakia but Odening and Gräfner (1979) have shown that the material was infact Paramphistomum ichikawai. The known intermediate hosts of O. streptocoelium, O. dicranocoelium and O. scoliocoelium are Glyptanisus (=Gyraulus) gilberti in Australia (Durie, 1953) and Bulimus pulchellus in India (Jain, 1969); Anisus natalensis (now Ceratophalus natalensis) in Kenya (Dinnik, 1951) and Bulimus pulchellus in India (Mukherjee and Chauhan, 1965; Jain and Srivastava, 1969) respectively.

All the three species of the genus Leiperocotyle are African and the host genera are solely African, L. okapi and L. congolense in the okapi (Okapia johnstoni) and L. gretillati in Syncerus caffer. Porter (1947)(as cited by Round, 1968) has reported an unidentified Paramphistomum species from a girrafe (Girrafa camelopardalis) that died in the London Zoo and as far as the writer is aware, this is the only record of a paramphistomid in this animal. The girrafe is related to the okapi and both belong to the same family, the Girrafidae. Although their present distribution is restricted to Africa, fossil girrafids are known from Asia in the Meiocene and Pleistocene and several groups reached eastern Europe in the Lower Pliocene (Darlington, 1963).

The monotypic genus Bilatorchis has so far been recorded in only two African host genera, Kobus and Limnotragus.

Among the paramphistomid genera occurring in ruminants, four are characterized by the presence of pharyngeal diverticula and because of this, they may be regarded as primitive. These genera are endemic in their occurrence as follows: Balanorchis (monotypic) in South America; Stephanopharynx (with three species but two of which are regarded here as synonyms) and Choerocotyloides (monotypic) in Africa and Olveria (with two species) in India.

Paramphistomids of ruminants probably have originated in tropical Asia. From here they were dispersed by their hosts to several regions and in these regions evolved into genera and several species and flourished especially in Africa where the climate is warm. It is believed that a land bridge existed during the late Miocence between Asia and Africa and fossil records appear to suggest that families and tribes of animals invaded Africa from Asia.

Hosts and localities of the various paramphistomid species studied in this work

This list has been compiled from literature and also includes new records of materials examined in this study. It does not attempt however to present a true and accurate picture of the geographical limits of these species or their range of hosts because it was not possible to check the accuracy of identification of all reports. Some previous reports were not accompanied by any description or illustration and the original materials are no longer available for re-examination. Where records were doubtful and where identifications were found later to be incorrect either by other authors or in this work, such records were not included in this list. Reports drawn merely from previous records and not based on new materials were also excluded.

Paramphistomum Fischoeder, 1901

1. *Paramphistomum cervi* (Zeder, 1790) Fischoeder, 1901

Alces alces	Newfoundland, Canada	Threlfall (1967)
	Ontario, Canada	Lankaster, Snider & Jerrad (1979)
	Buryat, Mongolia	Machul'skii (1950)
	Sweden	Nilsson (1971)
	Khabarovsk, USSR	Kadenatsii (1963)
	Kirov, USSR	Aleksandrova (1962)
	Tartar, USSR	Evranova (1955)
	Yakutsk, USSR	Gubanov (1964)
Bos taurus	Brazil	Velázquez-Maldonado (1976)
	Great Britain	Willmott (1950b)

Bos taurus	Nova Scotia & British Columbia, Canada	Swales (1933)
	Czechoslovakia	Present work
	Germany	Odening, Bockhardt & Gräfner (1978); Present work
	Turkey	Present work
	Briansk Oblast, USSR	Sivtseva (1963)
	Moldavia, USSR	Zgardan & Frukhtman (1965)
	Volhynia Oblast, USSR	Podlesnii (1962)
Cattle	Bulgaria	Vishnyakov & Ivanov (1964); Popov, Bankov, Denev, Georgiev, Bratanov & Monov (1966)
	Czechoslovakia	Chroust (1964)
	Denmark	Present work
	Cheshire, England	Pillers (1922); Craig & Davies (1937)
	England	Present work
	France	Guilhon & Priouzeau (1945)
	Munich, Germany	Kraneburg (1977)
	Milanese region, Italy	Bonini (1963)
	Ireland	Kelly (1948); Present work
	Mongolia	Ivashkin (1978)
	Netherlands	Schoon (1947); Bos (1948); Rinses (1948); Present work
	Białystok, Poland	Wieczorowski (1971)
	Włodawsk, Poland	Anczykowski & Chowaniec (1955)
	Tulcea district, Rumania	Tudor & Anton (1968)

Cattle	Scotland	Willmott (1950b)
	USA	Price & McIntosh (1944)
	Chelyaniskaya Oblast, USSR	Toshchev (1949)
	Khabarovsk, USSR	Kadenatsii (1963)
	Siberia, USSR	Toshchev (1949)
	Serbia, Yugoslavia	Babić (1966)
	Yugoslavia	Mikačić (1938)
Bos grunniens	Mongolia	Ivashkin (1978)
	Tibet	Present work
Capra a. aegagrus	Azerbaidzhan, USSR	Azadov (1960)
Goat	Mongolia	Ivashkin (1978)
Capreolus capreolus	Czechoslovakia	Pav (1962)
	Munich, Germany	Kraneburg (1978)
	Sweden	Nilsson (1971)
	Georgia, USSR	Rodonaya (1962)
	Primorsk region, USSR	Oshmarin & Oparin in Oshmarin (1963)
Capreolus pygargus	Khabarovsk region, USSR	Kadenatsii (1963)
	Yakutsk, USSR	Gubanov (1964)
Capreolus sp.	Germany	Odening, Bockhardt & Gräfner (1978)
Cervus canadensis asiaticus	Khabarovsk region, USSR	Kadenatsii (1963)
Cervus elaphus	Austria	Present work
	Czechoslovakia	Pav (1962); Present work
	Germany	Schultze-Rhonhof (1972)
	Poland	Zadura (1960)
Cervus elaphus xanthopygus	Primorsk region, USSR	Oshmarin & Oparin in Oshmarin (1963)
Cervus nippon	Primorsk region, USSR	Oshmarin & Oparin in Oshmarin (1963)

Cervus nippon hortulorum	Far-eastern, USSR	Ovcharenko (1963)
Dama dama	Czechoslovakia	Pav (1962)
Ovis aries	Tirana, Albania	Dodbiba (1969)
	Azerbaidzhan, USSR	Asadov (1960)
	Moldavia, USSR	Zgardan & Frukhtman (1965)
Ovis musimon	Bulgaria	Popov, Bankov, Denev, Georgiev, Bratanov & Monov (1966)
	Czechoslovakia	Mottl & Pav (1958); Pav (1962)
	Mongolia	Ivashkin (1978)
	Tulcea, Rumania	Tudor & Anton (1968)
	Turkey	Merdivenci (1959)
	Khabarovsk region, USSR	Kadenatsii (1963)
	Yugoslavia	Vujić (1965)
Rangifer tarandus	Chukotsky Natsional'ny Okrug, USSR	Mitskevich (1963)
	Khabarovsk region, USSR	Kadenatsii (1963)
Rangifer tarandus caragasi	Khabarovsk region, USSR	Kadenatsii (1963)

2. Paramphistomum gracile Fischoeder, 1901

Bos kerabau	Sri Lanka	Fischoeder (1901, 1902, 1903)
Bos indicus	Sri Lanka	Näsmark (1937)
Cattle	Japan	Fukui (1922)
	Sri Lanka	Von Linstow (1906)
Boselaphus tragocamelus	Sri Lanka	Fischoeder (1901, 1902, 1903); Näsmark (1937)
Ovis sp.	Bangkok, Thailand	Present work
Domestic ruminants	India	Sey (1979)

3. Paramphistomum liorchis Fischoeder, 1901

Blastocerus dichotomus	Brazil	Fischoeder (1901, 1902, 1903); Travassos (1934); Näsmark, (1937)
Dorcelaphus campestris	Brazil	Fischoeder (1901, 1902, 1903); Travassos (1934)
Mazama americana	Brazil	Näsmark (1937)
	Mato Grosso, Brazil	Present work
Mazama namby	Brazil	Fischoeder (1901, 1902, 1903); Travassos (1934); Näsmark (1937); Present work
Mazama rufina	Brazil	Fischoeder (1901, 1902, 1903); Travassos (1934)
Mazama simplicicornis	Brazil	Fischoeder (1901, 1902, 1903); Travassos (1934); Present work
Ozotoceros bezoarticus	Brazil	Näsmark (1937)
Odocoileus mexicanus	Brazil	Fischoeder (1901, 1902, 1903); Näsmark (1937)
Odocoileus virginianus	Alabama, Florida, Georgia, Lousiana, South Carolina, USA	Prestwood, Smith & Mahan (1970)
Deer	Florida & Lousiana, USA	Price & McIntosh (1944)
Cattle	Florida & Lousiana, USA	Price & McIntosh (1944)

4. Paramphistomum epiclitum Fischoeder, 1904

Bos indicus	Saigon, Vietnam	Fischoeder (1904)
	Rangoon, Burma	Present work
	Calicut, Kerala, India	Gupta & Nakhasi (1977a)
Cattle	Dacca Bangladesh	Present work
	Punjab, India	Gupta (1963)
	India	Present work
	Lahore, Pakistan	Näsmark (1937)
Bubalus bubalis	Saigon, Vietnam	Fischoeder (1904); Näsmark (1937); Railliet (1924)
	Punjab, India	Gupta (1964)
	India	Present work
	Malaysia	Lee & Lowe (1971)
	Lahore, Pakistan	Näsmark (1937)
Capra hircus	Burma	Present work
Goat	Rangoon, Burma	Present work
Sheep	India	Bhattacharyulu & Pande (1969); Present work
Domestic ruminants	India	Sey (1979)

5. Paramphistomum gotoi Fukui, 1922

Bos taurus	Japan	Fukui (1922b, 1926, 1929); Näsmark (1937)
	Philippines	Present work
	Kuibyshev Oblast, USSR	Sivtseva (1963)
Cattle	Kyoto, Japan	Yamaguti (1939)
	Pusan, Korea	Chu (1972)
Bubalus bubalis	Egypt	Sey (1976, 1977)
	India	Mukerjee & Chauhan (1965)
	Philippines	Present work

Ovis aries	Mongolia	Pačenovský, Hovorka & Krupicer (1975)
Sheep	Hong Kong	Present work
Domestic ruminants	Rumania	Sey (1978)

6. Paramphistomum ichikawai Fukui, 1922

Bos taurus	Australia	Durie (1951)
	China	Fukui (1926, 1929); Näsmark (1947)
	Czechoslovakia	Present paper
	Kagoshima, Japan	Fukui (1922c, 1926, 1929)
	Berlin & Hannover, Germnay	Present work
	Pusan, South Korea	Present work
	Taiwan (Formosa)	Fukui (1926, 1929), Näsmark (1937)
	Ukraine, USSR	Mereminskii, Gluzman & Artemenko (1968)
Bos taurus brachyceros	Bulgaria	Mikhailova, Gateva & Nedeva (1972-73)
Cattle	Australia	Present work
	Berlin & Cottbus, Germany	Odening, Bockhardt & Gräfner (1978)
	Southern Moravia, Czechoslovakia	Kotrlá & Chroust (1978)
	Hungary	Sey (1974)
	Belorussia, USSR	Egorov & Meshkova (1974)
	Blagoveshchensk, USSR	Katkov (1971)
	Ukraine, USSR	Erbolatov (1974); Gluzman & Artemenko(1969); Gluzman (1972); Meremens-kii (1972); Klesov & Meremenskii (1973)
	USSR	Davydova-Velichko (1964); Present work

Cattle	Serbia, Yugoslavia	Vujić (1965); Babic (1966)
Capra hircus	China	Present work
Ovis aries	Czechoslovakia	Pačenovský, Hovorka & Krupicer (1976)
Sheep	New South Wales, Australia	Boray (1969, 1971)
	Czechoslovakia	Pačenovský, Hovorka & Krupicer (1976)
	Hungary	Sey (1974)
	Belorussia, USSR	Egorov & Meshkova (1974)
	Kazakhstan, USSR	Erbolatov (1974)
	Ukaraine, USSR	Klesov & Meremenskii(1973)
	Yugoslavia	Vujić (1965)
Domestic ruminants	Rumania	Sey (1978)

7. Paramphistomum leydeni Näsmark, 1937

Bos taurus	Königsberg (now Kaliningrad, USSR)	Näsmark (1937)
	Brazil	Velázquez-Maldonado (1976); Present work
	Hamburg & Hanover, Germnay	Present work
	USSR	Present work
Cattle	Brazil	Present work
	Hungary	Sey (1974)
	Utrecht, Netherlands	Present work
	U. Skraastad, Norway	Present work
	Turkey	Present work
	Venezuela	Present work
	Serbia, Yugoslavia	Babić (1966)
Cervus elaphus	Austria	Present work
Sheep	Hungary	Sey (1974)
	Yugoslavia	Vujić (1965)

8. Paramphistomum hiberniae Willmott, 1950

Bos taurus	England	Present work
	Ireland	Willmott (1950b); Present work
	Channel Islands	Willmott & Pester (1955)
	Netherlands	Willmott (1950b)
	Scotland	Willmott (1950b)
Cattle	Byansk region, USSR	Nikitin (1971)
	Karakalpak, USSR	Ruziev (1970)

9. Paramphistomum cephalophi n. sp.

Cephalophus nigrifrons	Visoke, Virunga	Present work
	Rwanda	

Calicophoron Näsmark, 1937

1. Calicophoron calicophorum (Fischoeder, 1901) Näsmark, 1937

Axis axis	India	Present work
Bos indicus	Burma	Present work
	Uttar Pradesh, India	Mukherjee & Chauhan (1965)
	Malaysia	Lee (1967); Present work
	Sri Lanka	Näsmark (1937); Present work
	Vietnam	Present work
Bos taurus	Queensland, Australia	Fischoeder (1901); Näsmark (1937); Durie (1951); Present work
	China	Fischoeder (1901)
	Uttar Pradesh, India	Mukherjee & Chauhan (1965)
	Kyoto Japan	Yamaguti (1939)
	New Zealand	Present work

Bos taurus	Korea	Present work
	Philippines	Present work
Bos sp.	Malaysia	Lee & Lowe (1971)
Cattle	Australia	Kelly & Henderson (1973); Brotowidjoyo & Copeman (1979); Present work
	Fiji	Present work
	Hong Kong	Present work
	Bihar, India	Varma (1957)
	Solomon Islands	Present work
	Sri Lanka	Seneviratna (1955); Present work
	Thailand	Present work
	Azerbaidzhan, USSR	Davydova (1959)
	Khabarovsk region, USSR	Kadenatsii (1963)
Bubalus bubalis	Bihar, India	Varma (1957)
	Bareilly, India	Mukherjee (1966)
	Uttar Pradesh, India	Mukherjee & Chauhan (1965)
	Urimo, Papua New Guinea	Present work
	Philippines	Eduardo & Manuel (1975); Eduardo (1976)
	Sri Lanka	Crusz (1952); Seneviratna (1955)
	Saigon, Vietnam	Railliet (1924)
Capra hircus	Fiji	Present work
	Korea	Present work
	Sri Lanka	Seneviratna (1955)
	Taiwan	Present work
	Vietnam	Present work
Goat	Bihar, India	Varma (1957)
Cervus axei	Altay, USSR	Velichko (1973)

Ovis aries	Queensland, Australia	Näsmark (1937) Present work
	Chandigarh, India	Gupta & Gupta (1977); Gupta & Nakhasi (1977a)
	Uttar Pradesh, India	Mukherjee & Chauhan (1965)
Sheep	Bihar, India	Varma (1957)
	Jammu & Kashmir, India	Bali (1972)
	Astrakhan, USSR	Davydova (1959)
Rangifer tarandus	Murmansk region, USSR	Velichko (1973)

2. Calicophoron bothriophoron (Braun, 1892) n. comb.

Bos indicus	Cameroon	Graber, Fernagut & Oumatie (1966); Sey & Graber (1979b)
	Madagascar	Braun (1892); Fischoeder (1901); Näsmark (1937); Grétillat (1958)
	Mwanza, Tanzania	Present work
Bos taurus	Fort Lamy, Chad	Grétillat (1960)
Cattle	Tanarive, Madagascar	Present work
	Mauritius	Present work
	Low Uebi Scebeli River, Somalia	Gentile, Scisioli & Sobrero (1980)
	Merca, Somalia	Present work
	Lake region, Tanzania	Dinnik (1964)
Capra hircus	Kenya	Round (1962); Present work
Kobus defassa	Kenya	Present work
	Manyama, Tanzania	Present work
Syncerus caffer	Kenya	Present work
Sheep	Nanyuki, Kenya	Present work

3. Calicophoron microbothrium (Fischoeder, 1901) n. comb.

Aepyceros melampus	Botswana	Present work
	Tanzania	Ashizawa, Kono, Nosaka, Usui & Tateyama (1971)
	Zimbabwe	Present work
Alcelaphus buselaphus cokei	Mazabuka, Zambia	Present work
Bos indicus	Chad	Graber (1969); Present work
	Cameroon	Graber, Fernagut & Oumatie (1966)
Bos taurus	Fort Lamy & Bongor, Chad	Grétillat (1960)
	Egypt	Näsmark (1937); Sey (1977)
	Portugal	Caeiro (1961)
	Sardinia	Present work
	Republic of South Africa	Present work
Bos sp.	Kenya	Round (1962)
	Uganda	Bwangamoi (1968)
Cattle	Botswana	Present work
	Cairo, Egypt	Present work
	Khuzistan, Iran	Arfaa (1962)
	Iraq	Present work
	Israel	Lengy (1960)
	Kenya	Dinnik and Dinnik (1962)
	Madagascar	Prod'hon, Richard, Brygoo & Daynes (1968)
	Mozambique	Present work
	Sardinia	Reinhardt (1969); Sey & Arru (1977)
	Tanzania	Dinnik (1964); Butler & Yeoman (1962)

Cattle	Republic of South, Africa	Present work
	Uganda	Dinnik and Dinnik (1956)
Bubalus bubalis	Egypt	Näsmark (1937); Sey (1976, 1977)
	Khuzistan, Iran	Arfaa (1962)
Bovidae	Zaire	Van Strydonck (1970)
Capra hircus	Ati & Abecher, Chad	Grétillat (1960), Graber (1969)
	Egypt	Sey (1977)
Capra nubiana	Egypt	Sey (1977)
Goat	Angola	Present work
	Corsica	Present work
	Sardinia	Sey & Arru (1977)
	Sudan	Abdel-Malek (1959)
Camellus dromedarius	Egypt	Sey (1977)
Damaliscus dorcas	Cape Town, Republic of South Africa	Present work
Damaliscus korrigum	Chad	Graber (1969)
Gazella dorcas	Cairo, Egypt	Fischoeder (1901); Näsmark, (1937)
Gazella thomsonii	Mkalama, Tanzania	Yeh (1956)
Gazella rufifrons	Chad	Graber (1969)
Hippotragus equinus	Chad	Graber (1969)
	Republic of South, Africa	Present work
	Sudan	Present work
	Upemba National Park, Zaire	Prudhoe (1957)

Kobus defassa	Chad	Graber (1969)
Kobus defassa crawshayi	Upemba National Park, Zaire	Prudhoe (1957)
Kobus ellipaiprymnus	Zambia & Zimbabwe	Roth & Dalchow (1967)
Kobus leche	Zimbabwe	Present work
Kobus varondi	Upemba National park, Zaire	Prudhoe (1957)
Oryx gazelle	Chad	Graber (1969)
Ovis aries	Bongor & Abecher, Chad	Graber (1969)
	Egypt	Sey (1977)
	Kenya	Round (1962)
Ovis sp.	Iraq	Present work
	Republic of South Africa	Present work
Sheep	Angola	Present work
	Chad	Graber (1969)
	Cairo, Egypt	Present work
	Kenya	Roach & Lopes (1966)
	Khuzistan, Iran	Arfaa (1962)
	Baghdad, Iraq	Present work
	Israel	Lengy (1960)
	Zaria, Nigeria	Van Veen Schillhorn & Bida (1976)
	Republic of South Africa	Present work
	Sudan	Abdel-Malek (1959)
Redunca arundinum	Zambia and Zimbabwe	Roth & Dalchow (1967)
Redunca redunca	Lake Rukwa, Tanzania	Present work
Redunca redunca nigeriensis	Chad	Graber (1969)

Syncerus caffer	Kruger National Park, Republic of South Africa	Basson, McCully, Kruger, Van Niekerk, Young & de Vos (1970)
	Uganda	Dinnik, Walker, Barnett & Brocklesby (1963)
	Upemba National Park, Zaire	Prudhoe (1957)
Syncerus caffer aequinoctialis	Chad	Graber (1969)
Taurotragus oryx	Kenya	Present work
	Upemba National Park, Zaire	Prudhoe (1957)

4. Calicophoron papillosum (Stiles and Goldberger, 1910) Näsmark, 1937

Bos indicus	Punjab, India	Stiles & Goldberger (1910)
	Sanawar, India	Mukherjee & Chauhan (1965)
Cattle	Karachi, Pakistan	Khan (1963)
Bubalus bubalis	Dacca, Bangladesh	Present work
	Lucknow & Madras, India	Gupta (1965a); Gupta & Nakhasi (1977a); Present work
	Indonesia	Present work
	Karachi, Pakistan	Khan (1963)
Buffalo	Hue, Vietnam	Railliet (1924)

5. Calicophoron papilligerum (Stiles and Goldberger, 1910) n. comb.

Cervus eldi	? (probably India)	Stiles & Goldbgerger (1910)

6. Calicophoron raja Näsmark, 1937

Aepyceros melampus	Botswana	Present work
	Serengeti, Tanzania	Present work
Alcelaphus buselaphus cokei	Serengeti, Tanzania	Present work
Bos indicus	Chad	Present work
	Lake Region, Tanzania	Dinnik (1964); Present work
	Republic of South Africa	Present work
Bos taurus	Cuba	Present work
	Kenya	Round (1962); Present work
	Pretoria, Republic of South Africa	Present work
Cattle	Botswana	Present work
	Kenya	Present work
	Komatipoort, Republic of South Africa	Present work
	Sudan	Näsmark (1937)
	Uganda	Dinnik & Dinnik (1956)
	Mazabuka, Zambia	Present work
Capra hircus	Lochinvar, Zambia	Present work
	Zimbabwe	Present work
Connochaetes taurinus	Namibia	Present work
	Mazabuka, Zambia	Present work
	Zimbabwe	Present work
Damaliscus korrigum	Serengeti, Tanzania	Present work
Gazella thompsonii	Serengeti, Tanzania	Present work
Kobus defassa	Serengeti, Tanzania	Present work
Kobus leche	Botswana	Present work
Kobus varondi	Botswana	Present work
	Tanzania	Present work

Oryx gazelle	Namibia	Present work
Ovis sp.	Naval's Point, Republic of South Africa	Present work
	Mwanza, Tanzania	Present work
	Mbesuma, Chinsali, Zambia	Present work
Redunca redunca	Tanzania	Present work
Syncerus caffer	Namibia	Present work
	Tanzania	Sachs & Sachs (1968)
	Namwala, Zambia	Present work
	Zimbabwe	Present work
Taurotragus oryx	Serengeti, Tanzania	Present work
Tragelaphus scriptus	Zimbabwe	Present work
Tragelaphus strepsiceros	Zimbabwe	Present work
Antelopes	Tanzania	Sachs and Sachs (1968)

7. Calicophoron clavula (Näsmark, 1937) n. comb.

Aepyceros melampus	Selous game reserve, Tanzania	Present work
Alcelaphus buselaphus	Selous game reserve, Tanzania	Present work
Bos indicus	Cairo, Egypt	Näsmark (1937)
	Chad	Sey & Graber (1969b)
	Republic of Niger	Sey & Graber (1969b)
	Mwanza, Tanzania	Present work
Cattle	Somalia	Sobrero (1962)
Bovidae	Zaire	Van Strydonck (1970)

Capra hircus	Batha, Chad	Present work
Hippotragus equinus	Katagum, Nigeria	Present work
	Sudan	Present work
Hippotragus niger	Selous game reserve Tanzania	Present work
Kobus defassa	Sudan	Näsmark (1937)
	Garamba, Zaire	Näsmark (1937)
Kobus defassa harnieri	Parc National de la Garamba, Zaire	Present work
Kobus kob	Sudan	Näsmark (1937)
	Faradje, Zaire	Näsmark (1937)
Kobus varondi	Kasongo, Zaire	Manter & Pritchard (1964)
Redunca bohor	Sudan	Näsmark (1937)
	Faradje, Zaire	Näsmark (1937)
Syncerus caffer	Selous game reserve Tanzania	Present work
	Acholi, Uganda	Present work
Sheep	Somalia	Sobrero (1962)

8. Calicophoron microbothrioides (Price and McIntosh, 1944) n. comb.

Cattle	Cuba	Present work
	Bulgaria	Kamburov, Vasilev, Samnaliev & Kanev (1977); Samnaliev (1980)
	Puerto Rico	Present work
	USA	Price & McIntosh (1944)

9. Calicophoron sukari (Dinnik, 1954) n. comb.

Bos indicus	Lake Region, Tanzania	Dinnik (1954); Present work
Bos taurus	Nairobi, Nanyuki, Nakuru, Kenya	Dinnik (1964)
Bos sp.	Kenya	Round (1962)
Cattle	Cubreza Sul, Angola	Dinnik (1965)
	Ethiopia	Present work
	East Africa	Dinnik (1965)
	Lake Region, Tanzania	Dinnik (1964)
	Uganda	Dinnik & Dinnik (1956, 1957); Present work
	Zambia	Dinnik (1965);Present work
Goat	Tanzania	Dinnik (1965)
Sheep	Ethiopia	Dinnik (1965); Present work
	Zambia	Dinnik (1965)
Syncerus caffer	Tanzania	Sachs & Sachs (1968); Present work
	Zambia & Zimbabwe	Roth & Dalchow (1967)
Antelopes	Central Africa	Grétillat (1964b)
	Tanzania	Sachs & Sachs (1968)

10. Calicophoron phillerouxi (Dinnik, 1961) n. comb.

Aepyceros melampus	Serengeti, Tanzania	Present work
Bos indicus	Chari, Baguirmi, Chad	Present work
	Kenya	Dinnik (1961)
	Mauritius	Dinnik (1961)
	Republic of Niger	Sey & Graber (1969b)
	Lake Region, Tanzania	Dinnik (1961);Present work
	Mazabuka, Zambia	Dinnik (1961)
	Zimbabwe	Dinnik (1961)

Bos taurus	Kenya	Round (1962)
	Uganda	Bwangamoi (1968)
Cattle	Mauritius	Dinnik (1965);Present work
	Kabala, Freetown Sierra Leone	Present work
	Lake Region, Tanzania	Dinnik (1964)
	Komatipoort, Republic of South Africa	Present work
	Chinsali, Mazabuka, Zambia	Present work
Damaliscus korrigum	Serengeti, Tanzania	Present work
Hippotragus equinus	Zambia & Zimbabwe	Roth & Dalchow (1967)
Kobus defassa	Serengeti, Tanzania	Present work
Kobus defassa harnieri	Zaire	Present work
Kobus kob	Uganda	Dinnik (1963);Present work
Kobus varondi	Lake Rukwa, Tanzania	Present work
Redunca arundinum	Zambia & Zimbabwe	Roth & Dalchow (1967)
Redunca redunca	Mazabuka, Zambia	Present work
Syncerus caffer	Central African Republic	Sey & Graber (1979b)
	Tanzania	Sachs & Sachs (1968); Present work
	Uganda	Dinnik, Walker, Barnett & Brocklesby (1963); Present work
	Mazabuka & Namwala, Zambia	Present work
	Zambia & Zimbabwe	Roth & Dalchow (1967)
	Parc National Albert & Parc National de la Garamba, Zaire	Present work

Tragelaphus strepticerus	Central Africa	Roth & Dalchow (1967)
Antelopes	Tanzania	Sachs & Sachs (1968)

11. Calicophoron daubneyi (Dinnik, 1962) n. comb.

Bos indicus	Somalia	Present work
Bos taurus	Naivasha & Muguga, Kenya	Dinnik (1962)
	Greece	Present work
	Bolu, Trukey	Present work
Cattle	Bulgaria	Sey & Vishnyakov (1976)
	Postdam, Germany	Odening, Bockhardt & Gräfner (1978)
	Aquila & Rome abattoirs, Italy	Present work
	Sardinia	Sey & Arru (1977)
Bubalus bubalis	Mengen, Turkey	Present work
Buffalo	Bulgaria	Sey and Vishnyakov (1976)
Goat	Sardinia	Sey & Arru (1977)
Sheep	Bulgaria	Sey & Vishnyakov (1976)
	Sardinia	Sey & Arru (1977)
	Aquila abattoir, Italy	Present work
	Kenya	Roach & Lopes (1966)
Domestic ruminants	Rumania	Sey (1978)

12. Calicophoron sukumum (Dinnik, 1964) n. comb.

Bos indicus	Sukumaland, Tanzania	Dinnik (1964);Present work
Bos taurus	Cuba	Present work
	Mazabuka, Zambia	Present work
Connochaetes taurinus	Serengeti, Tanzania	Present work

Damaliscus korrigum	Serengeti, Tanzania	Present work
Hippotragus equinus	Zambia & Zimbabwe	Roth & Dalchow (1967)
Kobus defassa	Serengeti, Tanzania	Present work
Kobus leche	Zambia	Present work
Redunca arundinum	Zambia & Zimbabwe	Roth & Dalchow
Syncerus caffer	Tanzania	Sachs & Sachs (1968); Present work
	Zambia & Zimbabwe	Roth & Dalchow (1967)
	Mazabuka & Fort Jameson, Zambia	Present work
Taurotragus oryx	Serengeti, Tanzania	Present work
Antelopes	Tanzania	Sachs & Sachs (1968)

Gigantocotyle Näsmark, 1937

1. Gigantocotyle gigantocotyle (Brandes, 1896) Näsmark, 1937

Hippopotamus amphibius	Africa	Brandes in Otto (1896)
	Kruger National Park, Republic of South Africa	McCully, Van Niekerk & Kruger (1967)
	Transvaal, Republic of South Africa	Swart (1961)
	Sudan	Present work
	Uganda	Bwangamoi (1968)
	Kasai, Zaire	Näsmark (1937); Dollfus (1963)
	Parc National de la Garamba, Zaire	Present work
	Zambia	Present work

2. Gigantocotyle formosanum (Fukui, 1929) Näsmark, 1937

Bos taurus	Taiwan	Fukui (1929); Näsmark (1937); Present work
	Japan	Näsmark (1937)
Bubalus bubalis	India	Present work
	Masbate, Philippines	Present work
	Vietnam	Present work
Domestic buffalo	Canton, China	Yeh (1957)

3. Gigantocotyle symmeri Näsmark, 1937

Bos indicus	Cameroon	Graber, Fernagut & Oumatie (1966); Present work
Cattle	Sudan	Näsmark (1937); Present work
Kobus leche	Botswana	Present work
	Zambia	Present work
Limnotragus spekei	Zimbabwe	Present work
Syncerrus caffer	Central African Republic	Sey & Graber (1979b)

4. Gigantocotyle duplicitestorum Näsmark, 1937

Hippopotamus amphibius	Transvaal, Republic of South Africa	Swart (1961)
	Uganda	Näsmark (1937); Dinnik, Walker, Barnett & Brocklesby (1963); Present work
	Sudan	Näsmark (1937)
	Chinsali & Chambesi, Zambia	Present work

Explanatum (Fukui, 1929) status emended

1. Explanatum explanatum (Creplin, 1847) Fukui, 1929

Bos banteng	Indonesia	Adiwinata (1955)
Bos indicus	Indonesia	Adiwinata (1955)
	Malaysia	Dawes (1936); Euzeby (1957)
Bos taurus	Indonesia	Adiwinata (1955)
Cattle	Burma	Chatterji (1938)
	Cambodia	Bergeon (1965)
	China	Cheng & Yang (1958)
	Assam, India	Thaper (1956)
	Bihar, India	Jha, Singh, Jha & Sinha (1977)
	Haryana, India	Sadana, Gupta, Mahajan & Kuchroo (1977)
	India	Srivastava (1944); Mukherjee & Chauhan (1965)
	Iraq	Kadhim, Altaif & Hawa (1969, 1970)
	Japan	Ashizawa, Nosaka, Yamaguchi, Kono, Inagaki & Osato (1968)
	Korea	Ashizawa, Nosaka, Inagaki & Yamaguchi (1968)
	Lahore, Pakistan	Gupta (1951)
	Karachi, Pakistan	Khan (1963)
	Philippines	Tubangui (1947)
	Sri Lanka	Seneviratna (1955); Present work
Bubalus bubalis	Bihar, India	Varma (1957)
	Lucknow, India	Gupta (1966)
	Saharanpur, India	Gupta & Nakhasi (1977a)
	Indonesia	Adiwinata (1955)

Bubalus bubalis	Malaysia	Dawes (1936); Euzeby (1957)
	Philippines	Tubangui (1947)
	Sri Lanka	Seneviratna (1955); Present work
Buffalo	Afghanistan	Present work
	Burma	Chatterji (1938)
	Assam & Bihar, India	Thapar (1956)
	India	Srivastava (1944); Singh (1958); Mukherjee & Chauhan (1965); Shanker & Singh (1978); Present work
	Iraq	Leiper (1957)
	Baghdad, Iraq	Kadhim, Altaif & Hawa (1969, 1970); Kurtpinar & Latif (1970)
	Peshawar, Pakistan	Yusuf & Chaudry (1970)
	Annam, Vietnam	Railliet, Henry & Bauche (1914)
	Saigon, Vietnam	Railliet (1924)
	Sri Lanka	Crusz (1952); Kulasiri & Seneviratne (1956)
Capra hircus	Malaysia	Dawes (1936)
Goat	Patna, Bihar, India	Singh & Kuppuswany (1969)
	Uttar Pradesh, India	Katiyar & Varshney (1963)
	India	Thapar (1956); Mukerjee & Chauhan (1965); Shanker & Singh (1978)
	Iraq	Present work
Cervus unicolor	Orissa, India	Patnaik & Acharjyo (1970)
Cervus unicolor niger	Kanan State, India	Rao & Acharjo (1969)
Ovis aries	Assam & Bihar, India	Thapar (1956)
	Uttar Pradesh, India	Katiyar & Varhney (1963)

2. Explanatum bathycotyle (Fischoeder, 1901) Yamaguti, 1958

Axis axis ceylonensis	Sri Lanka	Shipleyi (1903)
Bos banteng	Indonesia	Kraneveld & Douwes (1940)
Bos indicus	Rangoon, Burma	Present work
	Sri Lanka	Willmott (1950a)
Bos taurus	Philippines	Present work
	Vietnam	Näsmark (1937)
Cattle	India	Gupta (1951)
	Sri Lanka	Crusz (1952)
	Saigon, Vietnam	Railliet (1924)
Bubalus bubalis	Indonesia	Kraneveld & Douwes (1940)
	Kuwait (host of Indian origin)	Present work
	Saharanpur, India	Gupta & Nakhasi (1977a)
	Maharasthra, India	Ghafoor (1970)
	Malaysia or Thailand	Lee & Lowe (1971)
	Philippines	Present work
	Sri Lanka	Shipleyi (1903); Näsmark (1937); Crusz (1952)
	Saigon, Vietnam	Näsmark (1937)
Buffalo	Annam, Vietnam	Railliet, Henry & Bauche (1914); Railliet (1924)
Goat	China	Maxwell (1921)
	India	Jain (1969)

3. Explanatum anisocotylea (Faust, 1920) Yamaguti, 1958

Bos taurus	Philippines	Schwartz (1925)
Bubalus bubalis	Philippines	Faust (1920), Schwartz (1925), Tubangui (1947)
	India	Present work
Goat	Taiping, Malaysia	Present work

Cotylophoron Stiles and Goldberger, 1910

1. Cotylophoron cotylophorum (Fischoeder, 1901) Stiles and Goldberger, 1910

Alcelaphus buselaphus	Chad and Central Africa	Graber (1969)
Axis axis	Orissa, India	Patnaik & Acharjyo (1970)
Bos indicus	Africa	Fischoeder (1901)
	Chad	Graber (1969)
	India	Varma (1957)
	Kenya	Dinnik (1956); Present work
	Malawi	Fitzsimmons (1964)
	Malaysia	Dawes (1936), Euseby (1957)
	Mwanza, Tanzania	Dinnik (1964);Present work
Bos taurus	East Africa	Fischoeder (1901)
	Angola	Serrano (1962)
	Egypt	Nagaty (1942)
	Philippines	Schwartz (1925); De Jesus (1938)
	Venezuela	Caballero y Caballero & Diaz-Ungria (1958)
	Kivu & Urundi, Zaire	Dollfus (1950)
Bos sp.	Hangchow, China	Wu (1937)
	Kenya	Round (1962)
	East Africa	Maplestone (1923)
	Philippines	Tubangui (1947)
	Uganda	Bwangamoi (1968)
Cattle	Angola	Caeiro (1961)
	Burma	Chatterji (1938); Griffiths (1957)
	India	Singh & Lakra (1971)
	Cambodia	Bergeon (1965)
	Karachi, Pakistan	Rahman (1958); Khan (1963)

Cattle	Shanghai, China	Wu & Chen (1941)
	Soochow, China	Hsu (1935)
	Kenya	Present work
	Rwanda	Fain & Ramée (1949)
	Lake region, Tanzania	Dinnik (1964)
	Annam, Vietnam	Railliet, Henry & Bauche (1914)
	Zaire	Stunkard (1929)
	Zambia	LeRoux (1931)
Bovidae	Zaire	Van Strydonck (1970)
Bubalus bubalis	Cairo, Egypt	Nagaty (1942)
	Bihar, India	Varma (1957)
	Malaysia	Euzéby (1957)
	Philippines	Schwartz (1925); De Leon & Juplo (1966)
Buffalo	Shanghai, China	Wu & Chen (1941)
	China	Chen (1935)
	India	Thapar (1956); Shah & Pandit (1959); Mukherjee & Chauhan (1965)
	Pakistan	Khan (1963)
	Peshawar, Pakistan	Yusuf & Chaudry (1970)
	Uganda	Dinnik & Dinnik (1956)
Capra hircus	China	Chen (1935)
	Chad	Graber (1969)
	Burma	Bhattacharjee (1937)
	Bihar, India	Varma (1957)
	Liberia	Szidat (1932)
	Malawi	Fitzsimmons (1964)
	Malaysia	Dawes (1936); Euzéby (1957)
	Uganda	Bwangamoi (1968)
Goat	India	Shah & Pandit (1959); Katiyar & Varshney (1963); Mukherjee & Chauhan (1967); Deorani & Katiyar (1967)

Goat	Kenya	Dinnik & Dinnik (1956)
	Pakistan	Rahman (1958); Khan (1963)
	Philippines	Manuel & Madriaga (1966)
Cephalophus harveyi	Uganda	Bwangamoi (1968)
Damaliscus korrigum	French East Africa	Dollfus (1950)
	Chad	Graber (1969)
Hippotragus equinus	Zambia & Zimbabwe	Roth & Dalchow (1967)
Hippotragus niger	Zambia & Zimbabwe	Roth & Dalchow (1967)
Kobus defassa	Chad	Graber (1969)
	Zaire	Van Strydonck (1970)
Kobus defassa crawshayi	Upemba National Park, Zaire	Prudhoe (1957)
Kobus kob	Zaire	Stunkard (1929)
	Uganda	Bwangamoi (1968)
Kobus ellipsiprymnus	Uganda	Bwangamoi (1968)
Kobus leche	Zaire	Manter & Pritchard (1964)
Kobus varondi	Zaire	Manter & Pritchard (1964)
	Upemba National Park, Zaire	Prudhoe (1957)
Ovis aries	Chad	Graber (1969)
	Cairo, Egypt	Nagaty (1942)
	Bihar, India	Varma (1957)
	Kenya	Round (1962)
	Malawi	Fitzsimmons (1964)
	Uganda	Bwangamoi (1968)
Sheep	Burma	Chatterji (1938)
	Chad	Graber (1965)
	India	Thapar (1956); Shah & Pandit (1959)

Sheep	India	Balasubramaniam, Anandan, Ganesakale & Alwar (1973)
		Anandan, Viswanathan, Balasubramaniam & Alwar (1974)
	Shanghai, China	Wu & Chen (1941)
	Karachi, Pakistan	Khan (1963)
	New York, USA	Price & McIntosh (1944)
	Zambia	LeRoux (1931)
Syncerus caffer	Chad	Graber (1969)
	Republic of South	Basson, McCully, Kruger, Van Niekerk, Young & De Vos (1970)
	Tanzania	Sachs & Sachs (1968)
	Uganda	Dinnik, Walker, Barnett & Brocklesby (1963)
	Zaire	Gretillat (1966)
	Zambia & Zimbabwe	Roth & Dalchow (1967)
	Upemba National Park, Zaire	Prudhoe (1957)
Taurotragus oryx	Uganda	Bwangamoi (1968)
	Zambia & Zimbabwe	Roth & Dalchow (1967)
	Upemba National Park, Zaire	Prudhoe (1957)
Tragelaphus scriptus	Zambia	Mettrick (1963)
	Upemba National Park, Zaire	Prudhoe (1957)
Tragelaphus strepticerus	Zambia & Zimbabwe	Roth & Dalchow (1967)
Antelopes	Tanzania	Sachs & Sachs (1968)

2. Cotylophoron jacksoni Näsmark, 1937

Alcelaphus buselaphus	Mount Elgon, East Africa	Näsmark (1937)
	Chinsali & Chunga, Zambia	Present work
Bos indicus	Mburara, Uganda	Present work
Bos taurus	Kenya	Round (1962)
Cattle	Gambia	Present work
	Kenya	Dinnik & Dinnik (1956)
	Uganda	Dinnik & Dinnik (1956)
Hippotragus niger	Tanzania	Present work
Tragelaphus strepsiceros	Zambia & Zimbabwe	Roth & Dalchow (1967)

3. Cotylophoron fuelleborni Näsmark, 1937

Aepyceros melampus	Malawi	Näsmark (1937
Booceros euryceros	Zaire	Van Strydonck (1970)
Bos indicus	Lake region, Tanzania	Dinnik (1964)
Bos taurus	Cameroon	Näsmark (1937)
Cattle	Kenya	Present work
	Lake region, Tanzania	Dinnik (1964)
	Mazabuka, Zambia	Present work
Bovidae	Rwanda & Zaire	Van Strydonck (1970)
Capra sp.	Cameroon	Näsmark (1937)
Cephalophus sp.	Cameroon	Näsmark (1937)
Syncerus caffer	Cameroon	Näsmark (1937)
	Uganda	Dinnik, Walker, Barnett & Brocklesby (1968)
Buffalo	Fort Jameson, Zambia	Present work

4. Cotylophoron panamensis Price & McIntosh, 1953

Bos taurus	Carimagua, Llanos Orientalis, Columbia	Present work
	Nagua, Provincia de Maria Trinidad Sanchez, Dominican Republic	Present work
Ovis aries	Panama	Price & MacIntosh (1953)

5. Cotylophoron bareilliense Mukherjee and Chauhan, 1965

Bos indicus	Mahiyangana, Kandy Area, Sri Lanka	Present work
Bos taurus	Iloilo, Philippines	Present work
Bubalus bubalis	Pangasinan, Philippines	Present work
Capra hircus	Bareilly, India	Mukherjee & Chauhan (1965)
Sheep	India	Bhattacharyulu & Pande (1969)

6. Cotylophoron macrosphinctris Sey and Graber, 1979

Syncerus caffer	Central African Empire	Sey and Graber (1979)
	Acholi, Uganda	Present work
	Parc National de la Garamba, Zaire	Present work

7. Cotylophoron xiangjiangense Wang, 1979

Bubalus bubalis	Wu Lan, China	Wang, 1979

Orthocoelium (Stiles and Goldberger, 1910) Price and McIntosh, 1953

1. Orthocoelium orthocoelium (Fischoeder, 1901) Price and McIntosh, 1953

Bos indicus	Burma	Bhattacharjee (1937)
	Malaysia	Dawes (1936)
Bos taurus	Japan	Fukui (1929)
Bos sp.	Malaysia or Thailand	Lee & Lowe (1971)
Cattle	Burma	Chatterji (1938)
	Cambodia	Bergeon (1965)
	Shanghai, China	Chen (1937); Present work
	Bihar, India	Thapar (1956)
	Uttar Pradesh, India	Mukherjee & Chauhan (1965)
	Malaysia	Present work
	Hue, Vietnam	Railliet (1924)
Bubalus bubalis	Bangladesh	Present work
	Malaysia or Thailand	Lee & Lowe (1971)
	Philippines	Present work
	Sri Lanka	Fischoeder (1901); Näsmark (1937); Present work
	Vietnam	Näsmark (1937)
Buffalo	Canton & Shanghai, China	Chen (1937)
Capra hircus	Malaysia	Dawes (1936)
Goat	Japan	Ashizawa, Nosaka & Tateyama (1970)
Sheep	Shanghai, China	Chen (1937)
	India	Thapar (1956)
	Japan	Ashizawa, Nosaka & Tateyama (1970)
Swamp deer	India	Present work:

2. Orthocoelium streptocoelium (Fischoeder, 1901) Yamaguti, 1971

Bos indicus	Malaysia	Lee (1967)
Bos taurus	Queensland, Australia	Durie (1951)
Bos sp.	Malaysia or Thailand	Lee & Lowe (1971)
Bubalus bubalis	Australia	Keith & Keith (1969)
	Borneo, Malaysia	Schad, Kuntz, Anteson & Webster (1964)
	Malaysia or Thailand	Lee & Lowe (1971)
	Sri Lanka	Fischoeder (1901);Näsmark (1937); Present work
Buffalo	Zaire	Van Strydonck (1970)
Capra hircus	Borneo, Malaysia	Schad, Kuntz, Anteson & Webster (1964)
Cervus unicolor	Australia	Keith & Keith (1969)
Kobus defassa	Zaire	Van Strydonck (1970)
Kobus thomasi	Zaire	Van Strydonck (1970)
Tragelaphus scriptus	Zaire	Van Stryndonck (1970)

3. Orthocoelium dicranocoelium (Fischoeder, 1901) Yamaguti, 1971

Bos indicus	Berlin Veterinary School, probably from Sri Lanka	Fischoeder (1901)
Bos taurus	Philippines	Present work
	Sri Lanka	Näsmark (1937); Present work
Cattle	Sri Lanka	Seneviratna (1955)
Bubalus bubalis	Lucknow, India	Gupta (1965a); Gupta & Nakhasi (1977b)
Goat	India	Present work
	Bareilly & Uttar, Pradesh, India	Jain (1969)

Sheep	Indonesia	Present work

4. Orthocoelium scoliocoelium (Fischoeder, 1904) Yamaguti, 1971

Bos indicus	Chad	Present work
	Lucknow, India	Gupta (1965a)
	Indonesia	Present work
	Malaysia	Lee (1967)
	Annam, Vietnam	Fischoeder (1904)
	Nakuru, Kenya	Dinnik (1956)
Bos taurus	China	Näsmark (1937)
	Calcutta, India	Näsmark (1937)
	Kyoto, Japan	Yamaguti (1939)
	Kenya	Present work
	Borneo, Malaysia	Schad, Kuntz, Anteson & Webster (1964)
	Philippines	Present work
Bos sp.	Malaysia or Thailand	Lee & Lowe (1971)
Cattle	Andhra Pradesh, India	Subbarao, Ventkataratnan, & Satyanarayanacharyulu (1969)
	Bengal, India	Mukherjee & Chauhan (1965)
	Karachi, Pakistan	Khan (1963)
	Nha-Trang, Vietnam	Railliet (1924)
Bubalus bubalis	Punjab, India	Näsmark (1937)
	Indonesia	Muchlis (1959)
	Macassar, Indonesia	Yamaguti (1954)
	Malaysia or Thailand	Lee & Lowe (1971)
	Saigon, Vietnam	Näsmark (1937)
Buffalo	Karachi, Pakistan	Khan (1963)
	Saigon & Nha-Trang, Vietnam	Railliet (1924)
Capra hircus	Nagano Prefecture, Japan	Yamaguti (1953)

Capra sp.	Meghalaya, India	Soota & Ghoshi (1977)
Goat	China	Maxwell (1921)
	Rithora & Bareilly, India	Jain & Srivastava (1969)
	Bengal, India	Mukherjee & Chauhan (1965)
	Kenya	Dinnik (1956); Round (1962)
Ovis aries	Calicut, India	Gupta & Nakhasi (1977b)
Sheep	India	Mukherjee & Deorani (1962)
	Bengal, India	Mukherjee & Chauhan (1965)
	Janmu & Kashmir, India	Bali & Fotedar (1972)

5. Orthocoelium parvipapillatum (Stiles and Goldberger, 1910) n. comb.

Bos indicus	Phrapatoom, Thailand	Stiles & Goldberger (1910); Railliet (1924)
Bubalus bubalis	Punjab, India	Present work
Sheep	Indonesia	Present work

6. Orthocoelium dawesi (Gupta, 1958) Yamaguti, 1971

Bos indicus	Calicut, Madras, India	Gupta (1958a); Gupta & Nakhasi (1977b)
	India	Present work
Ovis aries	Calicut, Madras, India	Gupta & Nakhasi (1977b)

7. Orthocoelium gigantopharynx (Schad, Kuntz, Anteson and Webster, 1964) n. comb.

Bubalus bubalis	Malaysia	Schad, Kuntz, Anteson & Webster (1964); Present work

Bubalus bubalis	Philippines	Present work
	Lucknow, India	Sey (1979)
Capra hircus	Borneo, Malaysia	Schad, Kuntz, Anteson & Webster (1964)

8. Orthocoelium bovini (Gupta and Gupta, 1970) Eduardo, 1980

Cattle	Ernakulam, India	Gupta & Gupta (1970)

9. Orthocoelium narayanai (Gupta and Gupta, 1972) Eduardo, 1980

Cattle	Ernakulam, India	Gupta & Gupta (1972a)

10. Orthocoelium indonesiense Eduardo, 1980

Bos indicus	Indonesia	Eduardo (1980b)
Ovis sp.	Indonesia	Eduardo (1980b)

11. Orthocoelium dinniki n. sp.

Bubalus bubalis	Philippines	Present work
Cattle	Shanghai, China	Present work
	Tokyo, Japan	Present work
Goat	China	Present work

Bilatorchis Eduardo, 1980

1. Bilatorchis papillogenitalis Eduardo, 1980

Kobus leche	Zambia	Eduardo (1980a)
Connochaetes taurinus	Zambia	Present work

Leiperocotyle Eduardo, 1980

1. Leiperocotyle okapi (Leiper, 1935) Eduardo, 1980

Okapia johnstoni	Zaire	Leiper (1935); Eduardo (1980c)

2. Leiperocotyle congolense (Baer, 1936) Eduardo, 1980

Okapia johnstoni	Zaire	Baer (1936, 1950)
	Ituri, Zaire	Van den Berghe (1937)
	Angunu, Zaire	Present work

3. Leiperocotyle gretillati nomen novum

Syncerus caffer (buffle noir)	Kasai, Lula, Central Africa	Grétillat (1966); Present work

Stephanopharynx Fischoeder, 1901

1. Stephanopharynx compactus Fischoeder, 1901

Bos indicus	Cameroon	Graber, Fernagut & Oumatie (1966)
	Chad	Graber (1969)
	Lake region, Tanzania	Dinnik (1964)
Bos taurus	Africa	Fischoeder (1901)
Cattle	Chad	Grétillat (1960)
	Mauritius	Dinnik (1965)
	Lake region, Tanzania	Dinnik (1964)
	Zambia	LeRoux (1934); Present work
Connochaetes taurinus	Monze, Zambia	Present work
Hippotragus equinus	Chad	Graber (1969)
	Zaire	Dollfus (1963)
	Zambia	Present work

Kobus kob	Chad	Graber (1969)
	Uganda	Bwangamoi (1968)
	Katagum, Nigeria	Present work
Kobus defassa	Chad	Graber (1969)
Kobus leche	Zambia	Wright, Southgate & Howard (1979)
Kobus varondi	Egypt	Ezzat (1945)
	Zambia	LeRoux (1934); Present work
Kobus sp.	Uganda	Maplestone (1923)
Redunca arundinum	Quimbango, Malanga, Angola	Present work
Redunca redunca	Chad	Graber (1969)
	Egypt	Ezzat (1945)
	Faradje, Zaire	Stunkard (1929); Näsmark (1937)
Syncerus caffer	Chad	Graber (1969)
	Central African Empire	Sey & Graber (1969)
Buffalo	Zaire	Van Strydonck (1970)

Balanorchis Fischoeder, 1901

1. Balanorchis anastrophus Fischoeder, 1901

Bos taurus	Argentina	Roveda & Ringuelet (1947); Szidat & Ostrowski de Núñez (1962)
	Brazil	Travassos (1922); Travassos, Pinto & Muniz (1927); Pinto & Lins de Almeida (1937)

Bos taurus	Rio Grande du Sul, Brazil	Amato & Gutierres (1974); Velázquez-Maldonado (1976)
	Mato Grosso, Brazil	Present work
Bovines	Argentina	Schiffo & Lombardero (1974)
	Uruguay	Calzada (1940)
Blastocerus dichotomus	Brazil	Fischoeder (1901)
	Mato Grosso, Brazil	Travassos (1922); Travassos, Pinto & Muniz (1927)
Odocoileus gymnotis	Venezuela	Vogelsang & Rodgriguez (1952); Caballero y Caballero & Diaz-Ungria (1958)

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ADDENDUM

Sey (1980) has recently described Orthocoelium saccocoelium as a new species from specimens which were deposited in the Geneva Museum of Natural History and obtained from a deer in Indochina. However, from the description and illustration provided, the species is identical with Orthocoelium orthocoelium (Fischoeder, 1901) Price and McIntosh, 1953. Unable to examine the types and other specimens of the latter species, he was not aware of the similarity of his specimens with O. orthocoelium. When differentiating his species with the latter, he only refered to the very brief description and without illustration of O. orthocoelium by Näsmark (1937) who erroneously refered its pharynx to the paramphistomum type. As already explained earlier in this work, the pharynx of O. orthocoelium is not of that type but of the orthocoelium type as defined in this work and this is also the type illustrated by Sey for his species. What Sey described as "pocket-like flares" of the caeca in his species could be the "accordion-like foldings" of the caecal wall when contracted as was observed in contracted specimens of O. orthocoelium in the present study. Sey's Fig. 1 strongly indicates that his specimen is contracted. In view of the above, there seems to be no justification in regarding O. saccocoelium as a valid species and it should fall as a junior synonym of O. orthocoelium.

REFERENCE:

SEY, O. (1980) Re-examination of an amphistome (Trematoda) collection deposited in the Geneva Museum with a description of Orthocoelium saccocoelium sp. n. Revue Suisse de Zoologie, 87, 431-437.